METAPOPULATION DYNAMICS AND LANDSCAPE ECOLOGY OF THE FLORIDA SCRUB-JAY, *APHELOCOMA COERULESCENS*

By

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Dedicated to my wife and best friend, Ellen Mary Thoms

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Florida's only endemic bird species, the Florida Scrub-Jay (*Aphelocoma coerulescens*), is rapidly disappearing throughout much of its range. A 1992-1993 statewide survey shows that it has effectively gone extinct in 10 of 39 formerly occupied counties in less than two decades. To characterize the spatial structure and vulnerability of the Florida Scrub-Jay throughout the state, I developed and applied a new method to describe the species' metapopulation structure. This method uses GIS-generated buffers based on documented dispersal distances to identify separate metapopulations and highly connected subpopulations called mainlands (extinction resistant), islands (extinction prone), or midlands (vulnerable to extinction). Of the 42 jay metapopulations identified, only five include mainlands; 21 consist only of extinction-prone islands. The resulting

classification reveals key subpopulations requiring special attention to maintain the long-term viability of the existing metapopulations.

I developed and applied a technique for measuring habitat features and estimating habitat quality over large areas using image processing and GIS methods. The technique showed that jays in central Florida had a strong preference for open sandy areas, and few or no pine trees. A proximity analysis showed that demographic performance decreased near forests. Measurement of habitat variables using this technique will be a valuable technique for habitat management and conservation.

I developed a spatially explicit, individual-based model to simulate the metapopulation dynamics of Florida Scrub-Jays. Special emphasis was placed on realistically modeling dispersal. I conducted a small radio-tracking study and used data from long-term studies to parameterize and validate the model. Stage-age structure and dispersal distances generated by the model showed good fit to field data.

I used this simulation model to investigate the viability of 21 major Florida Scrub-Jay metapopulations across the state. For each metapopulation I simulated 2 or more hypothetical reserve designs, ranging from a minimal design with only currently protected jays, to a maximal design containing all significant populations as of 1993. All habitat was assumed to be restored and fully occupied. Model results indicated that only 3 of 21 metapopulations would be adequately protected without further habitat acquisition. At least 4 metapopulations appear to be at great risk of extinction.

CHAPTER 1
INTRODUCTION

Historical Background

For most of geologic time, Florida lay under water, attached to what is now northern Africa. With the breakup of the super-continent, Gondwanaland, in the Mesozoic Florida rafted from Africa and become attached to North America. There she remained under water throughout the entire Age of Dinosaurs and well into the Cenozoic. Only recently, about 25 million years ago, Florida emerged from the sea. Never again would she become completely inundated, despite huge global fluctuations in sea level. She changed drastically in size and shape, however, due to the episodic transgressions and regressions of the seas caused by the waxing and waning of great ice sheets on the continents. As glaciers advanced southward, then retreated, they produced continental-scale changes in the climate. During high sea levels, mesic forests in Florida prospered, but with falling sea levels Florida became more and more desert-like. During such periods, arid conditions prevailed across most of the southern continent, and fauna and flora from the west were free to move to Florida along a Gulf coastal corridor. Among these western immigrants was a xeric-adapted bird originating from a widespread species known today as the Western Scrub-Jay (*Aphelocoma californica*). Exactly when this species first arrived in Florida is uncertain, but it must have been at least several million years ago. Having made it to Florida, this jay would become isolated from it's western counterpart by the development of extensive wetlands associated with the Mississippi

delta during the mid-Pleistocene. As conditions became more mesic, xeric habitat became reduced and isolated into desert-like islands within which a remarkable assemblage of organisms evolved. Among these organisms that diverged from their western kin is the Florida-Scrub Jay, the subject of this dissertation.

Not long after the most recent Wisconsin glacial retreat, a mere 12,000 years ago, nomadic people known as the Clovis entered North America from Siberia and encountered a continent largely or entirely devoid of humans. At that time the continent teemed with giant animals such as mammoths, mastodons, ostrich-size flightless birds, huge ground sloths, horses, camels, saber-toothed cats, and giant tortoises. This megafaunal scene rivaled anything seen today in Africa. Within 1,000 to 2,000 years all of these species and many more became extinct. Dozens of large vertebrates appear to have made their last stand in Florida, their demise apparently coinciding with the arrival of the Clovis. It remains uncertain whether humans were largely to blame for these extinctions, as the megafauna also faced great changes in climate and landscape. Yet, it is highly likely that humans contributed significantly to these megafaunal extinctions.

The Florida Scrub-Jay managed to survive this period of massive extinctions. But by the mid-20th century, a new threat to the fauna and flora of Florida appeared. Discoveries in applied sciences and engineering paved the way for the demise of the Florida Scrub-Jay and its scrub habitat. Among these were the discovery that citrus could be grown on the formerly worthless, sandy, infertile soils upon which Florida Scrub-Jay habitat grew. The invention of air conditioning made tolerable the Florida summers, ushering in an era of massive suburban sprawl, much of it devouring Florida Scrub-Jay habitat.

In 1969, Glen E. Woolfenden turned his ornithological focus on the Florida Scrub-Jay at the Archbold Biological Station. Thus began a continuous 31 year scientific study of this single organism, making it one of the most thoroughly studied wild bird species in the world. By 1975 his research on jays became a classic example of altruism cited prominently in E.O. Wilson's (1975) influential Sociobiology. In the mid-1970s Woolfenden teamed up with John W. Fitzpatrick, an ornithologist with a strong background in population modeling. In 1984, they produced a highly-acclaimed Princeton monograph (Woolfenden and Fitzpatrick, 1984) describing the demography and cooperative behavior of this intriguing bird. Today, the number of publications on this species approaches one hundred, and the Florida Scrub-Jay continues to be widely cited as a classic example of altruism (e.g. Krebs and Davies 1998). No brief summary can do justice to this large body of work. Nonetheless, a short review of the basic natural history of the Florida Scrub-Jay follows (consult Woolfenden and Fitzpatrick 1996 for an extensive list of references).

Biological Background

The Florida Scrub-Jay, Florida's only endemic bird species, is a disjunct, relict taxon separated by more than 1600 km from its closest western relatives (Woolfenden and Fitzpatrick 1984). This habitat specialist is restricted to a patchily distributed scrub community found on sandy, infertile soils--mostly pre-Pleistocene and Pleistocene shoreline deposits. The vegetation is dominated by several species of low-stature scrub oaks (Quercus spp.). Jays rely heavily on acorns for food, especially during the winter, when they retrieve thousands of acorns cached in open, sandy areas during the fall (DeGange et al. 1989). Florida Scrub-Jays show a strong preference for low, open

habitats with numerous bare openings and few or no pine trees (Breininger et al. 1991). These optimal habitat conditions are maintained by frequent fires (Abrahamson et al. 1984). Jays living in fire-suppressed, overgrown habitats have much poorer demographic performance than jays in optimal conditions (Fitzpatrick and Woolfenden 1986), leading rapidly to local extirpation unless the habitat is burned (Fitzpatrick et al. 1994).

Florida Scrub-Jays are monogamous, cooperative breeders that defend permanent territories averaging 10 ha per family (Woolfenden and Fitzpatrick 1984). They have a well-developed sentinel system, in which a family member watches for predators while others in the group engage in other activities such as foraging (McGowan and Woolfenden 1989). Young nearly always delay dispersal for at least one year, remaining at home as helpers. Dispersal distances from natal to breeding territories are extremely short for both sexes, and these movements within contiguous habitat average less than 1 territory for males and 3.5 territories for females (Woolfenden and Fitzpatrick 1984). Dispersal behavior is associated with greatly elevated mortality even within optimal habitat (Fitzpatrick and Woolfenden 1986), and many behavioral adaptations (e.g., cooperative breeding, sentinel system, delayed dispersal) suggest that predation is extremely important to both resident and dispersing jays (Woolfenden and Fitzpatrick 1984; Fitzpatrick and Woolfenden 1986; Koenig et al. 1992).

Objectives

Despite the many studies and enormous amount of information available on Florida Scrub-Jays, opportunities to contribution to this large body of knowledge are afforded by new technologies, which allow new types of data to be collected and new questions to be asked. I employ several of these new technologies in this dissertation,

including remote sensing, geographic information systems, radiotelemetry, and computer modeling. Prior to the early 1990s, Florida Scrub-Jay research was not focused on conservation issues. With the increasing destruction of scrub habitat, and the Federal listing of the Florida Scrub-Jay as a threatened species in 1987, much more emphasis has been placed recently on applied research, and a flurry of conservation-oriented publications have since appeared. My hope is to fill in a few of the existing gaps. Exemplifying a key goal of conservation biology, such efforts are made applicable to the real world by the large body of basic knowledge already available for this species. This prior body of knowledge also makes it possible to attempt to synthesize a variety of information in the form of a spatially explicit computer model. More than half of my time as a doctoral student has been spent developing this model.

Chapter 2 provides an analysis of the entire known distribution of the Florida Scrub-Jay from a metapopulation perspective, based on a statewide census conducted in 1992-1993. A new classification technique is developed to describe the spatial structure of the jay population. This technique is general in nature, and has implications for the conservation of other species as well as the Florida Scrub-Jay. Portions of this chapter have recently been published (Stith et al. 1996), and I wish to thank Island Press for permission to include that publication in its entirety (with modifications).

Chapter 3 narrows the focus to a local level and examines the landscape ecology of the Florida Scrub-Jay in central Florida. A team of researchers collected demographic variables for color-banded jays at Avon Park Air Force Range (APAFR), in Highland and Polk county. New computer technology--image processing and GIS--was used to correlate physical features with habitat quality from a Florida Scrub-Jay's perspective in

this area. The relationship between demographic variables and the remotely-sensed habitat variables were examined. At issue is the possibility of measuring habitat quality, and potential demographic success remotely, and across large areas.

Chapter 4 examines the difficult subject of dispersal and describes an approach used to simulate dispersal in an individual-based model (IBM) developed for this dissertation. Two types of dispersal are simulated by the IBM. A close-distance dispersal module mimics a "stay-home-and-foray" strategy that results in most dispersing jays settling close to their natal territory. This module incorporates many details of Florida Scrub-Jay biology documented by long-term color-band studies (Woolfenden and Fitzpatrick 1984), including sex and age dominance relations. A long-distance dispersal module simulates a "floater" strategy, which accounts for the infrequent, though potentially important, tendency of some jays to abandon their natal territory and move long distances, often between habitat patches and through hostile landscape matrices. Empirical data on long-distance dispersal are poor, and a simple field experiment was conducted with radiotelemetry to obtain information useful for modeling purposes. To induce behavior that might be similar to long distance dispersal, radio-collared jays were experimentally displaced kilometers away from their natal territories. Habitat preferences, movement abilities, and mortality rates were recorded and incorporated into the long-distance dispersal module. In combination, the close- and long-distance dispersal modules produced a dispersal and stage-age curve that closely resembled results of long-term data from Archbold Biological Station. A constraint analysis was used to place plausible bounds on several of the poorly known long distance dispersal parameters. This

analysis relied on data that suggested where successful dispersal from Archbold Biological Station could and could not take place.

Chapter 5 describes the complete individual-based, spatially explicit population model, which incorporates the dispersal algorithms described in chapter 4. The model provides a framework for integrating much of what is currently known about the Florida Scrub-Jay. Simulations take place on a landscape provided by a geographic information system (GIS) file. Non-dispersing jays occupy discrete territories. Both sexes are modeled, and individual jays progress through 5 stages (juvenile, 1-year helper, older helper, inexperienced and experienced breeder). Each territory has a separate set of demographic parameters assigned to each sex and stage. Breeder experience and presence of helpers may affect fecundity. Helpers monitor neighboring territories within their "assessment sphere" and vie for breeder openings; the outcome of such competition is determined by simple dominance rules. Helpers may leave on long distance dispersals, during which time mortality and movement varies depending on landcover type.

The statewide population of jays was divided into 21 metapopulations thought to be demographically isolated from each other (fig. 5-0). Two series of maps were developed for each metapopulation. One map type depicts jays and habitat as mapped in 1992-1993. A second map type, referred to as an "acquisition" map, depicts jays as they might exist if all habitat patches were restored to optimal conditions, and distinguishes among jays within protected areas, unprotected habitat patches, and suburban areas. Key habitat patches are labeled on the acquisition maps, and are cross-referenced in the text descriptions, tables, and recommendations.

A series of simulations were run for each metapopulation based on different reserve design scenarios. These scenarios ranged from a minimal configuration consisting of only currently protected patches (no acquisition option), to a maximal configuration consisting of all significant patches (complete acquisition option). For all simulations, the assumption was made that all protected areas were restored and properly managed, and that jays had demographic performance and densities typical of high quality habitat. These assumptions should be viewed as optimistic. Jays outside of protected areas were assumed to have poor demographic performance typical of suburban areas.

The output from the simulation runs included estimates of extinction, quasi-extinction (probability of falling below 10 pairs), and percent population decline. Comparisons of these results provided the basis for ranking the vulnerability of different metapopulations around the state. Metapopulations were ranked in terms of vulnerability assuming no further acquisition, and in terms of potential for improvement through acquiring all unprotected habitat. The proper uses and limitations of population modeling are discussed.

Chapter 6 synthesizes previous chapters, focusing on some of the limitations of metapopulation theory. The chapter closes by presenting a set of landscape rules that provide guidelines for developing a statewide Habitat Conservation Plan for the Florida Scrub-Jay. Adherence to these landscape rules would likely maintain the viability of different jay populations across the state, while allowing for further loss of jays to human development in some areas.

CHAPTER 2
CLASSIFYING FLORIDA SCRUB-JAY METAPOPULATIONS

Introduction

Metapopulation theory, now a major paradigm within conservation biology (Harrison 1994; Doak and Mills 1994), can be viewed as island biogeography theory applied to single species (Hanski and Gilpin 1991). Whereas application of island biogeography to conservation followed shortly after its creation (MacArthur and Wilson 1967), application of metapopulation theory lagged far behind its formalization by Levins (1969, 1970). Simberloff (1988) attributes its growing emergence to a shift in ecological and conservation focus, from analysis of species turnover to analysis of extinction in small populations of individual species. Describing real world metapopulations, however, remains problematic.

Harrison (1991) pointed out ambiguities in the term "metapopulation," and described four different configurations of habitat patches that could be called metapopulations. Reviewing field studies of patchy systems, Harrison found few natural examples that matched Levins' original concept of a metapopulation. Recently, Harrison (1994) argued that metapopulation theory often is not applicable, such as cases where populations are highly isolated, highly connected, or so large as to be essentially invulnerable. She warned that: "the metapopulation concept is being taken seriously by managers, and taken too literally could lead to the 'principles' that single, isolated populations are always doomed, or that costly strategies involving multiple connected

reserves are always necessary" (p. 126). Doak and Mills (1994) reviewed the different metapopulation classes described by Harrison and held that "it will often be difficult or impossible to distinguish between these alternatives, and thus to assess the importance of metapopulation dynamics" (p. 624). They also warned that spatially explicit population models (SEPMs) simulating metapopulation dynamics typically use parameters that are difficult to measure in the field. Their list of required data included within-patch demographic rates and variances, temporal and spatial correlation of vital rates among populations, and dispersal distances and success. Harrison (1994) also stressed the difficulty of identifying all local populations and suitable habitat, and of estimating extinction and colonization rates among patches.

Although still controversial (e.g., Harrison, Stahl and Doak 1993), the metapopulation concept does provide a useful framework for describing the spatial structure of real populations. The concept, after all, is grounded on two of the most robust empirical generalizations in ecology and conservation biology: 1) extinction rates decrease with increasing population size, and 2) immigration and recolonization rates decrease with increasing isolation (MacArthur and Wilson 1967; Hanski 1994).

Our goal in this chapter is to illustrate how the above two generalizations can be used 1) to characterize quantitatively the metapopulation structure of a species, and 2) to develop "landscape rules" for conserving metapopulations of a declining species.

We begin with the results of a range-wide survey of the federally Threatened Florida Scrub-Jay (*Aphelocoma coerulescens*), conducted in 1992-1993. This species is patchily distributed, and thereby presents a challenging case study for describing

metapopulation structure. We offer a method for doing so using a detailed spatial database, combined with existing biological information and GIS technology. The technique uses computer-generated buffers, at several distances reflecting the dispersal behavior of the species, to delineate subpopulations with differing degrees of connectivity. Extinction vulnerability of each subpopulation is estimated via a PVA model (in our case, that of Fitzpatrick et al. 1991). We propose a simple nomenclature for classifying Florida Scrub-Jay metapopulations based on subpopulation size and connectivity. We conclude by deriving a few, metapopulation-based "landscape rules" that may be incorporated into a statewide framework for conservation plans affecting this rapidly declining bird species.

Statewide Survey of the Florida Scrub-Jay

Statewide Survey: Methods

The Florida Scrub-Jay was listed by the U. S. Fish and Wildlife Service (USFWS) as a Threatened species in 1987. In 1991 the USFWS notified landowners and county governments that clearing scrub could violate the Endangered Species Act (ESA) (USFWS 1991). At the same time, the USFWS began encouraging counties to develop regional Habitat Conservation Plans (HCP) that could solve local permitting problems by means of a single, biologically based, regional plan. To aid in this process, the USFWS partially sponsored the authors, and their cooperators, to conduct an intensive survey during 1992-1993 to document the range and sizes of subpopulations throughout the state, and to inventory existing potential habitat, whether occupied or not.

Our methods were similar to those used for the Northern Spotted Owl (Strix occidentalis caurina; Murphy and Noon 1992). Extensive prior information helped guide us. Cox (1987) had documented numerous jay localities throughout the state in the early 1980s, and had compiled historic records from diverse sources such as museums and Christmas Bird Counts. The Florida Breeding Bird Atlas (Kale et al. 1992) provided valuable data on jay sightings made by hundreds of volunteers from 1986 to 1991. Virtually all previously known jay localities were revisited for this survey. Information from the public was solicited through notices in magazines, newsletters, and newspapers. Additional, potential habitat patches were identified from U.S. Soil Conservation Service maps and aerial photographs, on which the white, sandy soil associated with jay habitat forms a distinctive signature.

Standard surveying techniques based on tape playback of jay territorial scolds (Fitzpatrick et al. 1991) were used to locate jays in habitat patches. Location and number of individuals in each group were plotted on field maps. The following qualitative habitat data were collected at most patches: occupancy by jays; estimated degree of vegetative overgrowth (1-4 scale); extent of human disturbance (1-4 scale); ownership status with respect to permanent protection from development. Time constraints prohibited making quantitative habitat measurements at the thousands of habitat patches visited. Although survey goals included attempting to find all known jay families outside of Federal lands, we know that a few jays were missed because of limited access to certain private lands. The total number missed, however, is not likely to exceed a few percent of the statewide population.

Federally-owned lands were not surveyed for this project. Those with large populations of jays include: Cape Canaveral Air Force Station, Merritt Island National Wildlife Refuge, Canaveral National Seashore, and Ocala National Forest. Florida Scrub-Jays at each of these areas are currently under study, so for the statewide summary we used estimates of numbers and locations of jays provided by the respective biologists conducting those studies.

To archive, map, and analyze the statewide data we developed a series of map layers by means of a GIS at Archbold Biological Station. PC and Sun ARC/INFO were used to input all GIS data (E.S.R.I. 1990). Habitat patches (both occupied and unoccupied) and jay locations, originally hand-drawn on soil or topographic maps (usually at 1:24000 scale), were digitized. Patch characteristics and jay family sizes were entered into accompanying data files. Map layers included current and historic range of jays, current distribution of suitable and potential habitat, and locations and numbers of jay families encountered.

Statewide Survey: Results

We estimate that as of 1993 the total population of Florida Scrub-Jays consisted of about 4,000 pairs (Fig. 2-1; Fitzpatrick et al. 1994). Both total numbers and overall geographic range have decreased dramatically during this century (Cox 1987). In recent decades the species has been extirpated from 10 of 39 formerly occupied counties, and it is now reduced to fewer than 10 pairs in 5 additional counties (detailed tabulations in Fitzpatrick et al., in prep.). Detailed, site-by site comparison of our survey with Cox's (1987) suggests that the species may have declined as much as 25% to 50% during the last decade alone.

Degraded quality of many currently occupied habitat patches suggests that further, substantial declines in the jay population are inevitable. Specifically, those jays occupying suburban areas (approximately 30% of all territories) are unlikely to persist as these suburbs continue to build out, given the rapid rate at which Florida's human population continues to expand. Furthermore, jays living in fire-suppressed, overgrown habitat (at least 2,100 families, or 64% of all occupied scrub patches by area) already are likely to be experiencing poor demographic performance (Fitzpatrick and Woolfenden 1986). These can be expected to decline further unless widespread restoration of habitat is begun soon.

A Method for Classifying Metapopulations

The patchy distribution and variable clustering of territories throughout the range of the Florida Scrub-Jay (Fig. 2-1) challenges us to expand upon traditional metapopulation concepts in order to describe the spatial structure of this species. In this section we describe our conceptual approach, and in the next we apply it to the Florida Scrub-Jay data.

Harrison's (1991) four classes of metapopulations can be presented graphically (Fig. 2-2) as different regions on a plot of degree of isolation against patch size distribution. Thus, Harrison's "non-equilibrium" metapopulation is that set of small patches in which each has a high probability of extinction, and among which little or no migration occurs. Local extinctions are not offset by recolonization, resulting in overall decline toward regional extinction. The "classical" model developed by Levins (1969, 1970) is a set of small patches which are individually prone to extinction, but which are

large enough and close enough to other patches so that recolonization balances extinction. "Patchy" metapopulations consist of patches so close together that migration among them is frequent, hence the patches function over the long run as a single demographic unit. Finally, the "mainland-island" model has a mixture of large and small patches close enough to allow frequent dispersal from an extinction-resistant mainland to the extinction-prone islands.

The lower right side of Fig 2-2. portrays two classes not presented by Harrison (1991). These large patches are either poorly-connected (i.e., "disjunct") or moderately-connected (i.e., "mainland-mainland"). Such large populations tend to be less interesting from a conservation standpoint, as they are essentially invulnerable to extinction.

Classifying metapopulations, therefore, requires species-specific information on both connectivity (i.e., dispersal behavior and barriers) and extinction probabilities (i.e., population sizes in patches), across space. For example, a system of small habitat patches might appear to support stable populations of certain organisms as "classical" or "patchy" systems, while other species might be "nonequilibrial" in the same system because of low density (hence small populations sizes) or limited dispersal ability.

Harrison's (1991) diagram of metapopulations represented connectivity among patches by means of a dashed line around those among which dispersal is frequent enough to 'unite the patches into a single demographic entity.' This boundary can be viewed as a 'dispersal buffer': an isoline of equal dispersal probability. Any number of patches may be included within a given dispersal buffer of a single subpopulation, provided that fragmentation is sufficiently 'fine-grained' (*sensu* Rolstad 1991). However, dispersal probability normally diminishes continuously (even if steeply) away from a

patch, and for most terrestrial species it asymptotically approaches zero at some point farther away than Harrison's single, discrete dispersal buffer. Therefore, we extend Harrison's diagrammatic approach by adding a second buffer to delineate the distance beyond which dispersal is effectively reduced to zero. *We maintain that this second buffer functionally identifies separate metapopulations.* We acknowledge that connectivity actually should be represented graphically as a continuous surface of dispersal probabilities. However, discrete boundaries, placed at biologically meaningful (and empirically determined) distances, greatly simplify the description of metapopulations. They also provide explicit, repeatable methodology for comparative or modeling purposes.

Harrison's metapopulation types may be characterized using these two buffers (Fig. 2-3). In "patchy" systems (Fig. 2-3a), every patch belongs to the same subpopulation, so they are all enclosed within a single, inner dispersal buffer. "Classical" systems (Fig. 2-3b) have small subpopulations separately encircled, representing the fact that each may go extinct temporarily, or may be 'rescued' before going extinct (Brown and Kodric-Brown 1977), both by way of colonization from another subpopulation enclosed within the outer buffer. The simplest "nonequilibrium" systems (Fig. 2-3c) are represented as bull's-eyes around small, isolated subpopulations. A "mainland-island" metapopulation (Fig. 2-3d) has a large subpopulation and several small ones within a single outer buffer.

The important point is that even more complicated patterns may be common in nature, arising from combinations or intermediate cases, and many of these are not easily fit into Harrison's (1991) four metapopulation classes. To deal with such complications,

we suggest characterizing metapopulations by describing the sizes of their constituent subpopulations. We propose a simple nomenclature, based on three key words --"island," "mainland," and "midland" --to characterize the relative sizes of the subpopulations within a metapopulation. Subpopulations small enough to be highly extinction prone in the absence of significant immigration are called 'islands.' Those large enough to be essentially invulnerable to extinction are called 'mainlands.' Intermediate sized subpopulations are neither extinction prone nor invulnerable to extinction. For lack of a better term, we refer to an intermediate size subpopulation as a 'midland.'

Distinctions among these categories need not be completely arbitrary. Species-specific population viability analysis (PVA) provides an explicit, quantifiable approach for describing subpopulations as extinction-prone, extinction-vulnerable, or extinction-resistant. Our introduction of the 'midland' category helps clarify the importance of turnover, which has been called the "hallmark of a genuine metapopulation dynamics" (Hanski and Gilpin 1991). Specifically, turnover is expected in systems with island-size subpopulations because they have high frequencies of extinction. But systems with midlands rather than islands are perhaps more often characterized by rescue rather than recolonization, as local extinctions will be rare. Thus, a system of midlands may exhibit little or no turnover even though no real mainlands are present, while a system of islands with the same degree of isolation may show high turnover. We agree with Sjogren (1991) in emphasizing the importance of rescue in metapopulation dynamics. Traditional emphasis on turnover probably resulted from the fact that rescue is much more difficult to measure empirically, as turnover only requires presence-absence data.

Harrison's metapopulation classes can be described using this island-midland-mainland nomenclature as follows: a "nonequilibrium" metapopulation is a system of one or more islands (i.e., extinction-prone subpopulations), with a total population size too small to persist. A "classical" metapopulation is a system of island-size subpopulations large enough and close enough together and of sufficient total size to allow persistence. Any system containing a midland or mainland (by definition) cannot be a nonequilibrium or classical metapopulation, as all subpopulations in the latter systems are extinction-prone. A "patchy" metapopulation is a set of patches close enough together to form a single subpopulation of sufficient size to persist (i.e. a midland or mainland). "Mainland-island" metapopulations are self-explanatory.

Explicit reference to 'midlands'--extinction-vulnerable patches of intermediate population size--produces metapopulation types not described in Harrison (1991). Systems with, for example, several midlands, or a mainland with several midlands, are possible. We illustrate some of these configurations by applying our nomenclature, quantitatively, to the Florida Scrub-Jay.

Metapopulation Structure of the Florida Scrub-Jay

Application of the above scheme to any species requires choosing two dispersal buffer distances and two threshold values for extinction-vulnerability among single populations. Here, for the Florida Scrub-Jay, we based each of these values on empirically gathered biological data. Buffer distances were derived from long-term field studies of marked individuals, and from information garnered on the statewide survey regarding occupancy of habitat patches at various distances from source populations.

Extinction vulnerability was estimated using a single-population viability model (Fitzpatrick et al. 1991). We then chose thresholds to delineate islands, midlands, and mainlands, much as Mace and Lande (1991) used extinction probabilities to propose IUCN threatened species categories.

Dispersal Distances

Between 1970 and 1993 we documented 233 successful natal dispersals from the marked population under long-term study at Archbold Biological Station (Figure 2-4; see also Woolfenden and Fitzpatrick 1984, 1986). Unlike the situation for most field studies of birds (e.g., Barrowclough 1978), many characteristics of our study and the behavior of jays themselves enhance our ability to locate dispersers that leave the main study area. Once established as breeders, for example, Florida Scrub-Jays are long-lived and completely sedentary. Furthermore, we have mapped in detail all scrub habitat within the local range of the species, and we census these tracts periodically in search of dispersed jays. (Such censuses reveal remarkably few banded dispersers among the many hundreds of jays encountered.) Because banded Florida Scrub-Jays from our study usually are tame to humans, both our own searches and casual encounters by local homeowners have high likelihood of exposing any off-site dispersers to us once they become paired on a territory. Indeed, if we assume that immigration and emigration rates are about equal in our study area, evidence suggests that we have succeeded in locating all but a low percentage of the jays that have departed over the 25-year period of our study. Therefore, although some dispersers do escape our detection, our observed dispersal curve (Fig. 2-4) can be only marginally biased toward the shorter distances.

About 80% of documented dispersals were within 1.7 km of the natal territory, 85% within 3.5 km, 97% within 6.7 km, and 99% within 8.3 km (Fig. 2-4). Data from field studies elsewhere in Florida reveal the same, remarkably sedentary dispersal behavior. The longest dispersal so far documented was a female we discovered pairing 35 km from her natal territory at Archbold, in 1994.

All dispersals we have documented around Archbold, including the longest one, involved jays that had moved either through continuous habitat or across gaps no greater than 5 km. To test the generality of this observation, we pooled dispersal information from the seven other biologists currently color-banding Florida Scrub-Jays around the state (D. Breininger, R. Bowman, G. Iverson, R. Mumme, P. Small, J. Thaxton, B. Toland, unpubl. data). Their studies, along with ours, cumulatively have produced about a thousand banded non-breeders that achieved dispersal age (Fitzpatrick et al., in prep.). Collectively these studies have documented only about 10 dispersals of 20 km or more, and only a few of these had crossed habitat gaps as large as 5 km. More important in the present context, despite ample opportunity to observe longer-distance movements, not a single example yet exists of a banded Florida Scrub-Jay having crossed more than 8 km of habitat that does not contain scrub oaks. We suspect that this distance is close to the biological maximum for the species.

Patch Occupancy

The observations just outlined suggest that for habitat specialists such as the Florida Scrub-Jay, dispersal curves measured in relatively contiguous habitat actually may overestimate the dispersal capabilities of individuals across fragmented systems. Direct behavioral observations strongly indicate that Florida Scrub-Jays resist crossing

large habitat gaps. Still, few opportunities exist to observe jays in the act of dispersing, hence the theoretical maximum dispersal-distance (i.e., the outer dispersal buffer) is extremely difficult to establish directly.

Seeking an indirect measure of dispersal frequencies across habitat gaps, we examined patch occupancy statewide as documented by our 1992-93 survey. We used Fragstats software (McGarigal and Marks 1994) to measure distances between each occupied patch of scrub habitat to its nearest neighboring, occupied patch. We then measured (by hand, as Fragstats cannot measure distances between patches of different attributes) the distances between each *unoccupied* suitable patch and the nearest *occupied* patch. For each distance class, the ratio of the count of the occupied-to-occupied distances to the total number of nearest neighbor distances yields the proportion of patches that are occupied at that distance away from occupied habitat.

Presumably, declines in patch occupancy with increasing distance to the nearest occupied habitat (Fig. 2-5) reflect diminishing recolonization rates following local extinctions. Occupancy remains above zero even at great distances, probably because larger isolated patches rarely experience extinction. This curve provides an empirical approach for delineating subpopulations and metapopulations: a subpopulation buffer is the maximum interpatch distance where occupancy rates remain high; the metapopulation buffer is the smallest interpatch distance where occupancy rates reach their minimum.

For Florida Scrub-Jays (Fig. 2-5) patch occupancy is about 90% to at least 2 km from a source, then declines monotonically to around 15% at 12 km. (Sample size of isolated patches decreased rapidly beyond 16 km, necessitating lumping of classes at the larger distances.) We infer from this occupancy curve that successful recolonization is a

rare event beyond about 12 km from an occupied patch of habitat. We use this distance to identify metapopulations that have become essentially demographically independent from one another (i.e., the outer dispersal-buffer).

We selected the distance of 3.5 km (about 2 miles) as an inner dispersal-buffer to delineate subpopulations. We choose this figure because: 1) behavioral information from a variety of sources, including radiotracking data (B. Stith, unpubl.), shows that jays begin to show reluctance to crossing habitat gaps at about this size (and at much smaller gaps where open water or closed-canopy forest are involved); 2) known dispersals of many banded jays included habitat gaps up to 3.5 km, but their frequency declines dramatically thereafter; 3) the observed dispersal curve from Archbold (Fig. 2-4) shows that in good habitat, more than 85% of dispersals by females, and fully 97% of those by males, are shorter than 3.5 km; 4) patch occupancy data (Fig. 2-5) show significant decline in colonization rates at distances above 3.5 km.

Population Viability Analysis

PVA based on a simulation model incorporating demographic (but not genetic) stochasticity and periodic, catastrophic epidemics (Fitzpatrick et al. 1991; Woolfenden and Fitzpatrick 1991) provided a quantitative method for defining boundaries along the island (extinction prone), midland (vulnerable), and mainland (extinction resistant) continuum (but see Taylor 1995). Among the several methods for expressing extinction vulnerability (e.g., Burgman et al. 1993; Boyce 1992; Caughley 1994) we elect the simple approach of specifying time-specific probability of persistence of populations of a given size.

Model results indicated that a population of jays with fewer than 10 breeding pairs has about a 50% probability of extinction within 100 years, while a population with 100 pairs has a 2% to 3% probability of extinction in the same time period. These two population sizes--10 and 100 pairs--provide convenient and biologically meaningful values by which to classify subpopulations as "islands" (< 10 pairs), "midlands" (10-99 pairs), and "mainlands" (> 99 pairs). Although subjectively chosen, these values effectively separate population sizes having fundamentally different levels of protection. These values also receive empirical support from several long-term bird studies (reviewed by Thomas 1990; Thomas et al. 1990; Boyce 1992).

Metapopulation Structure

We used a GIS buffering procedure (E.S.R.I. 1990) to generate dispersal-buffers around groups of jays occurring within 3.5 km (for subpopulations) and 12 km (for metapopulations) of each other (Fig. 2-6). We buffered jay territories rather than habitat patches because we strongly suspect that dispersing Florida Scrub-Jays cue on the presence of other, resident jays even more strongly than on habitat, so the functional boundaries of occupied patches may be determined by where actual jay families exist. We modified the resulting buffers in the following areas to reflect the presence of hard barriers to dispersal in the form of open water with forested margins: Myakka River, Peace River, St. Johns River, St. Lucie River, and Indian River Lagoon.

Using a 3.5 km dispersal-buffer we delineated 191 separate Florida Scrub-Jay subpopulations (Fig. 2-6). Over 80% (N=152 "islands") are smaller than 10 pairs (Fig. 2-7), and 70 of these consist of only a single pair or family of jays. Only 6 subpopulations contain at least 100 pairs ("mainlands"), leaving 32 "midlands" (10-99 pairs).

Using a 12 km dispersal-buffer we delineated 42 separate Florida Scrub-Jay metapopulations (Fig. 2-6). Again, most are small (Fig. 2-7). We tabulated the number and type of subpopulations within each metapopulation (Table 2-1), and noted how each metapopulation fits into Harrison's (1991) scheme.

Exactly half (21) contain fewer than 10 pairs, thereby constituting "nonequilibrium" systems. Along the north-central Gulf Coast (Fig. 2-8), for example, a group of non-equilibrium systems coincide with a heavily developed area containing a burgeoning human population. Only three Florida Scrub-Jay systems have configurations that may be "classical" metapopulations (i.e., contain only islands, but may be large enough to support one another following extinctions; e.g., Fig. 2-9). However, this technique provides no means of distinguishing "classical" systems from "nonequilibrium". Chapter 5 addresses this shortcoming using a simulation model. Another three systems represent "patchy" metapopulations (i.e., contain a single, fragmented subpopulation large enough for long-term persistence).

Five systems approximate "mainland-island" metapopulations, but each of these examples also contains at least one midland population (e.g., the large Lake Wales Ridge system, with one mainland, 10 midland, and 39 island populations; Fig. 2-10). These 10, plus 9 midland-island and one mainland-midland system, do not fit neatly any of Harrison's (1991) metapopulation classes.

A total of 32 midland populations exist (mean size=30.7), and these occur in 18 of the 42 separate metapopulations. Excluding the nonequilibrium systems, true islands are present in 17 systems. Therefore, assuming that dispersal is not inhibited by habitat loss

expanding the distances among patches, rescue (on midlands) may be at least as important as turnover (on islands) in Florida Scrub-Jay metapopulation dynamics.

Use of empirically derived dispersal-buffers and extinction probabilities provides an explicit method for quantitatively describing metapopulation structure. Application of this technique to the Florida Scrub-Jay demonstrates that a species can exhibit a variety of metapopulation patterns across its range. Patterns of aggregation and isolation do not conform to a single metapopulation class in the Florida Scrub-Jay. Such complex spatial structure is probably common in nature, particularly among species with large and widely dispersed populations restricted to a patchy habitat. Such patterns may be further complicated by perturbations of the natural system caused by humans.

Caveats

We offer several caveats as to the generality of dispersal-buffer methodology in conservation. (1) The technique is best suited for organisms occupying discrete territories, home ranges, or habitat patches amenable to mapping. (2) The technique is predicated on having a comprehensive survey. Missing data can lead to misleading results, especially as regards connections among metapopulations or subpopulations. (3) The technique presents a static, snapshot view of metapopulations. It does not easily reveal important dynamics among subpopulations, such as those obtainable from an SEPM. The viability of different configurations is best determined from SEPMs rather than single population PVAs. (4) Populations in decline or in "sinks" can present an overly optimistic picture (Thomas 1994). Indeed, we suspect that many of the "island" and "midland" subpopulations of Florida Scrub-Jays currently are failing to replace themselves demographically, as a result of habitat degradation from fire suppression.

Similarly, abnormally high densities may exist due to the "crowding effect" (Lamberson et al. 1992) following recent habitat losses. (5) The technique relies on numerous simplifying assumptions about dispersal behavior in defining connectivity among patches. Most important, it assumes random movement between patches, equal traversibility of interpatch habitats, absence of dispersal biases owing to habitat quality differences at the origin or the destination, and absence of density-dependence in behavior. More elaborate applications, of course, could incorporate alternative assumptions about these and other factors.

Another important consideration are the kinds of data to buffer. To create biologically meaningful--but very different--descriptions for the Florida Scrub-Jay we could have buffered around jay territories (our choice), occupied patches, suitable habitat patches both occupied and unoccupied, or all scrub habitat patches regardless of current suitability. Organisms such as Florida Scrub-Jays that are reluctant to become established in unoccupied, suitable habitat (e.g., Ebenhard 1991), or have high conspecific attraction or an "allee" effect (Smith and Peacock 1990) are best buffered around actual territories or occupied patches. This is because unoccupied sites have a low probability of becoming occupied regardless of their degree of isolation, hence contribute little to the current metapopulation dynamics of the species. On the other hand, excellent colonizers of empty habitat or species adept at long-distance dispersals via unoccupied stepping stones probably should be buffered around all habitat patches.

In summary, this method of classifying metapopulations provides a compact means of describing both connectivity and local population size through the use of simple terminology. Separate metapopulations are easily delineated using the maximum

dispersal buffer. The internal structure of each metapopulation is easily described using the inner dispersal buffer to delineate islands, midlands, and mainlands. Enumerating all metapopulations and describing their internal structure (table 2-1) reveals much about the distribution and viability of Florida Scrub-Jays. The differing internal configurations of metapopulations present different conservation problems and require different management approaches. Discussion of these matters is deferred until chapter 6, following the presentation of the modeling results (chapter 5) which analyze the viability of metapopulations around the state.

Note: This chapter has been published as Stith et al., 1996, and is reproduced with some modifications with the permission of Island Press.

Table 2-1. Summary information for 42 Florida Scrub-Jay metapopulations, including type of metapopulation, number of territories (pairs of jays), and number of subpopulations.

Metapopulation type (after Harrison 1991)	Metapopulation Type (Mainland, Midland, and/or Island) [a]			Size (pairs)	Number of subpopulations
Mainland-Island (?)	Mn	10Md	39I	1247	50
	Mn	Md	5I	1036	7
	Mn	Md	5I	466	7
	Mn	2Md	6I	237	9
	Mn	Md	5I	179	7
Unknown	Mn	Md		126	2
		4Md	11I	120	15
		2Md	I	103	3
		Md	5I	94	6
		Md	I	58	2
		2Md	3I	55	5
		Md	I	50	2
		Md	2I	29	3
		Md	3I	22	4
		Md	2I	18	3
Patchy		Md		26	1
		Md		22	1

Table 2-1 cont.

Metapopulation type (after Harrison 1991)	Metapopulation Type (Mainland, Midland, and/or Island) [a]	Size (pairs)	Number of subpopulations
	Md	15	1
Classical	16I	49	16
	10I	24	10
	6I	21	6
Nonequilibrium	3I	5	3
	3I	3	3
	2I	7	2
	2I	3	2
	2I	3	2
	2I	2	2
	2I	2	2
	2I	2	2
	I	6	1
	I	2	1[b]
	I	1	1[c]

[a] Numerical prefix indicates number of Mainlands (Mn), Midlands (Md), and Islands (I). See text for nomenclature.

[b] There was a total of 4 single Island systems composed of 2 pairs in one subpopulation.

[c] There was a total of 8 single Island systems composed of a subpopulation of one pair.

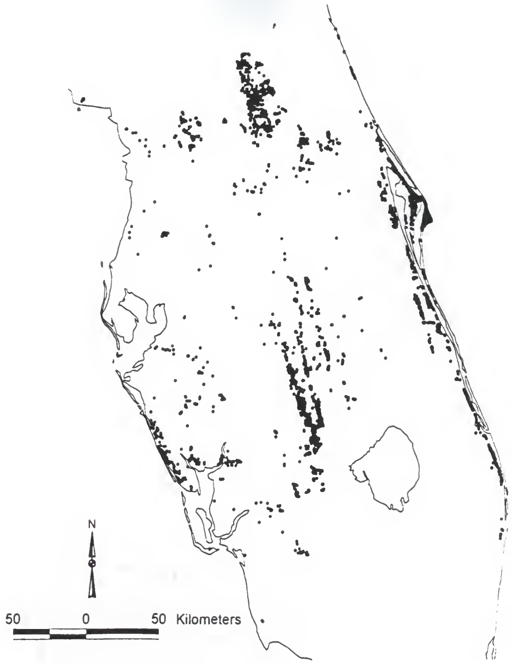


Fig. 2-1. 1993 distribution of Florida Scrub Jay groups (small black circles). Note the discontinuous distribution and variability in patterns of aggregation.

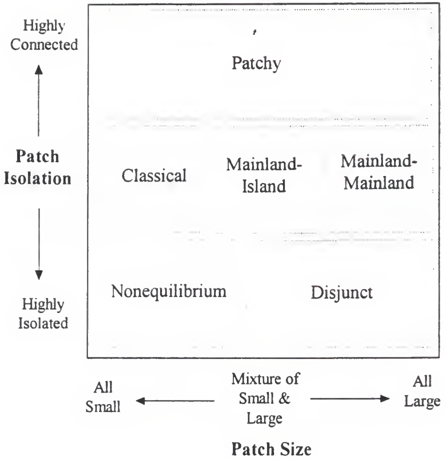


Fig. 2-2. Classification scheme showing different types of metapopulations based on patch size distribution (patches all small in size, mixture of small and large, and all large in size) along the horizontal axis, and degree of patch isolation (highly connected to highly isolated) on the vertical axis. Nonequilibrium, classical, mainland-island, and patchy classes are named according to Harrison (1991).

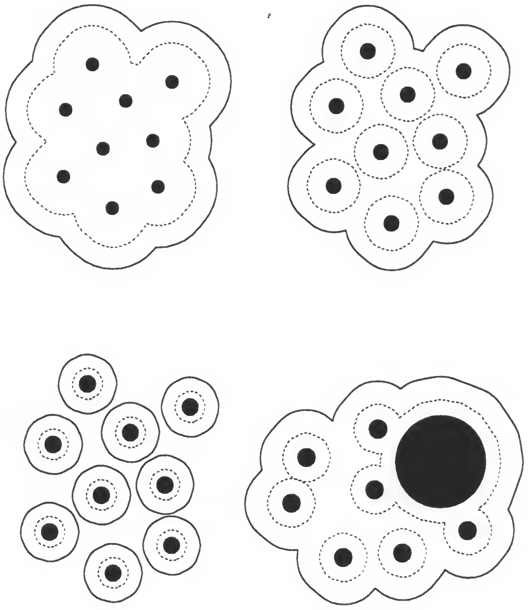


Fig. 2-3. Schematic depiction of different kinds of metapopulations, illustrating use of dispersal-distance buffers to predict recolonization rates among subpopulations. Dotted lines separate functional subpopulations, based on frequency of dispersal beyond them. Solid lines separate metapopulations, based on poor likelihood of dispersal among them. A. Patchy metapopulation. B. Classical metapopulation. C. Nonequilibrium metapopulations. D. Mainland-island metapopulation.

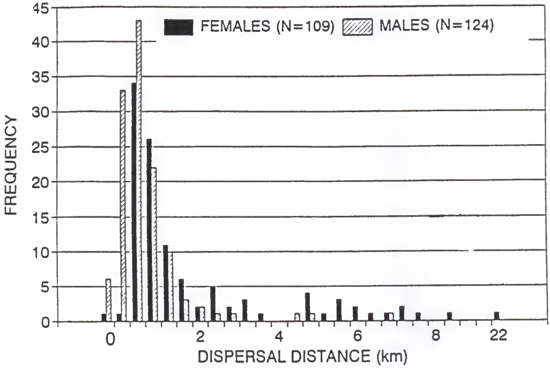


Fig. 2-4. Dispersal frequency curve. Dispersal distances from natal to breeding territories for color-banded jays at Archbold Biological Station, 1970-1993. About 85% of documented dispersals were within 3.5 km, and 99% within 8.3 km. The longest documented dispersal was 35 km.

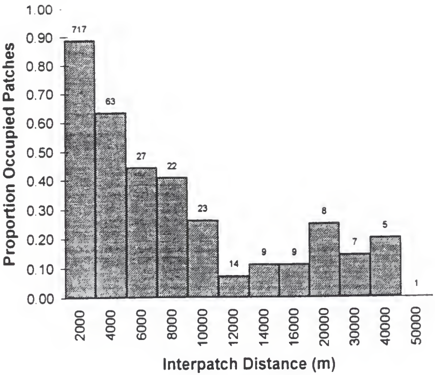


Fig. 2-5. Proportion of suitable habitat patches occupied by Florida Scrub-Jays as a function of their distance to the nearest separate patch of occupied habitat. Occupancy rates are high (nearly 90 %) for patches up to 2 km apart and decline monotonically to 12 km. Note the scale change after 16 km.

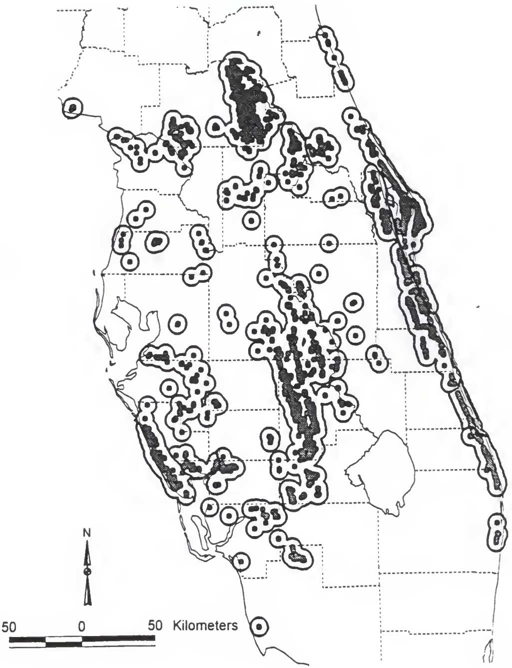


Fig. 2-6. Statewide jay distribution map with dispersal buffers. Shaded areas with thin, solid lines depict subpopulations of jays within easy dispersal distance (3.5 km) of one another. Thick lines delineate demographically independent metapopulations separated from each other by at least 12 km.

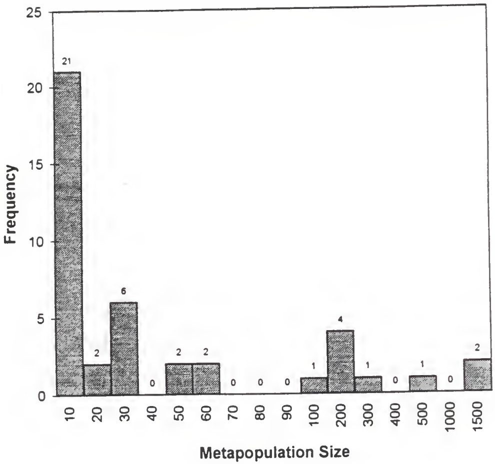


Fig. 2-7. Frequency of Florida Scrub-Jay metapopulation sizes. Note that 21 metapopulations have 10 pairs or less of jays. These represent nonequilibrium metapopulations.

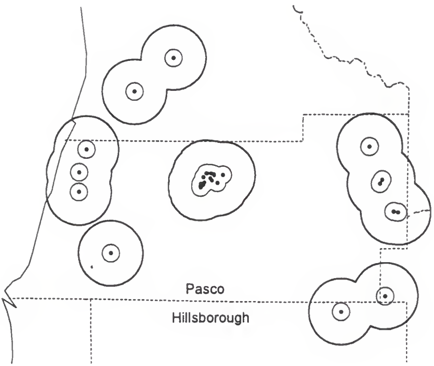


Fig. 2-8. Examples of non-equilibrium metapopulations from North Gulf coast. Each of the six metapopulations contains fewer than 10 pairs of jays, except for the centrally located system that contains a single, midland-size subpopulation.

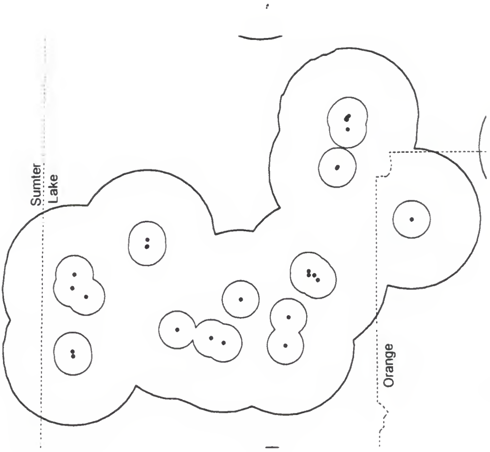


Fig. 2-9. Example of a "classical" metapopulation from five counties in Central Florida. Note the occurrence of jays in small islands of intermediate distance from one another.

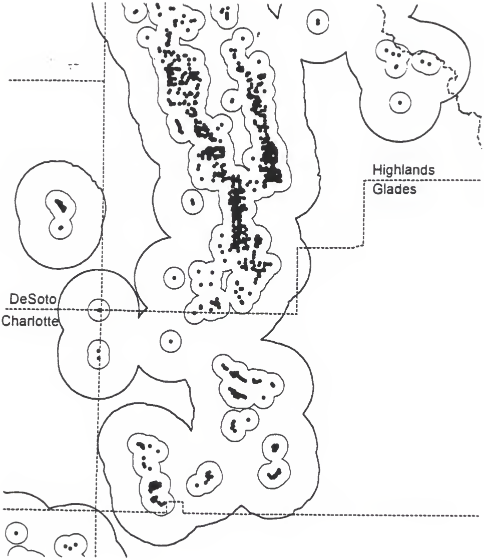


Fig. 2-10. Portion of the largest mainland-midland-island metapopulation in the interior, consisting of the Lake Wales Ridge and associated smaller sand deposits. The large central subpopulation (enclosed by the thin black line) contains nearly 800 pairs of jays. Small subpopulations to the south and east are within known dispersal distance of the large, central mainland. A small metapopulation to the west (in DeSoto County) contains a single subpopulation of 21 territories. This small system qualifies as a patchy metapopulation, since jays occur in two or more patches but the patches are so close together that they function as a single demographic unit.

CHAPTER 3
REMOTE SENSING OF FLORIDA SCRUB-JAY HABITAT

Introduction

The importance of understanding relationships between wildlife and habitat has been recognized for many decades (review in Morrison et al. 1992). The ultimate success of wildlife management and conservation efforts depends to a large degree on our ability to understand these relationships. Unfortunately, measuring habitat variables over large areas, and with sufficient spatial resolution to capture the essential habitat features a particular species responds to, is a difficult and time consuming task. In this chapter I apply a technique that greatly assists in the measurement and analysis of wildlife-habitat relationships across large areas. This technique, which relies heavily on recent advances in computer hardware and software technology, uses image processing and GIS software to measure habitat variables directly from scanned aerial photography.

Habitat requirements differ widely among most species, and choosing the appropriate habitat variables to measure is greatly facilitated for species whose habitat requirements are well understood. Long-term studies of the Florida Scrub-Jay have revealed much about the habitat requirements of this species (Woolfenden and Fitzpatrick 1984; Breininger et al. 1991, 1995, 1996). Research indicates that scrub-jays have a fairly simple "habitat template" consisting of low vegetation dominated by scrub oaks, open

sandy areas to cache acorns, and few or no pine trees. These habitat characteristics are naturally created and maintained by fire.

Pine tree density may be a critical factor in determining Florida Scrub-Jay habitat quality. Pine trees may affect scrub-jays indirectly in several fashions. Large trees provide perch sites and cover used by accipiters, important predators of jays. Pine trees probably reduce the effectiveness of the jays' sentinel system against aerial predators. A close competitor and nest predator, the Blue Jay, shows a strong preference for pine forests through much of the scrub-jays's range (Tarvin 1997). Competition between these two corvids may partially explain why Florida Scrub-Jays select open habitat (see discussion in Woolfenden and Fitzpatric 1984).

Declines in nesting success, and survival of juveniles and adults have been documented by Fitzpatrick and Woolfenden (1986) within a fire-suppressed habitat that gradually becomes overgrown. Jays living in open habitat have higher survival, nesting success, and larger mean group size than jays in less open habitat (Fitzpatrick and Woolfenden 1986; Breininger et al. 1995). Differences in these demographic traits may be due to habitat features immediately adjacent to jay territories (Breininger et al. 1996). Thus, although the internal quality of a jay territory may be high, territory position within the landscape mosaic may greatly influence demographic success.

In this chapter, I test some of these ideas using habitat features and demographic variables measured at the Avon Park Air Force Range (APAFR) in Polk and Highlands counties, Florida. I compare the habitat and demographic performance of jays occupying a north-south trending scrub ridge some 15 km in length. Jays along this ridge occupy habitat with different degrees of overgrowth and different adjacent habitat. The main

objective of this chapter is to test whether remote sensing can accurately measure habitat features that explain Florida Scrub-Jay demographic performance.

Methods

All image processing and GIS work was completed on a Sun workstation or an Intel 486-based PC using Arc/Info (ver. 4.3D) and Erdas (ver. 7.5) software.

Image Source

Regular color, black and white, and color infrared photography were evaluated for use in this project. Color infrared photography was flown for much of the APAFR through the NAPP program of the U.S.G.S. in March of 1994. I selected this photography for three primary reasons: separation between sandy and grassy areas was more distinct, wider coverage per frame made image mosaicing easier, and the photography is available for study sites outside of the APAFR that are currently under investigation for Florida Scrub-Jay conservation. Hence, results of this study could be extended to other areas.

Two photos covered the entire study area. Frame 6980-207 covered the area I refer to as N. Sandy Hill, which is between Kissimmee and Smith roads, and part of S. Sandy Hill south to Submarine Lake. Frame 6980-205 covered the remainder of S. Sandy Hill south to the southern fence line.

Image Scanning and Conversion

A Umax 1200 color scanner with a transparency adapter (for scanning positive or negative film; 600 dots-per-inch maximum hardware resolution) was used to scan the 1:40000 color transparencies at a resolution of 555 dots per inch, giving a ground resolution of approximately 1.8 meters (6 feet). Image-In scanning software provided by Umax for use with the scanner was used to scan all images on a PC.

Software from Earth Resource Data Analysis Systems (ERDAS) of Atlanta, Georgia was used to convert the TIFF files to ERDAS 7.5 LAN files.

Image Rectification and Mosaicing

I used ERDAS software to rectify the two images to Zone 17 of the Universal Transverse Mercator map projection using differentially corrected GPS points. I collected these GPS control points at various road intersections throughout the study area using a Trimble Pathfinder rover with a data logger. At each control point, 180 location measurements were acquired. I differentially corrected these control points using base files acquired from a Trimble Professional base station located on the APAFR. The mean of the 180 measurements taken at each control point was used as the final x and y coordinate for rectifying the images.

During the rectification process, I discarded some GPS points because their inclusion produced excessively high root mean square (RMS) errors. Several factors explain these high RMS errors. First, the expected error from the differentially corrected

GPS points (Trimble claims 2 to 5 m for the units I used) is substantial relative to the image resolution (2 m). Second, nonlinear distortions in the imagery owing to lens curvature, tilt angle, etc. cannot be corrected with this type of linear rectification process. Third, an error of one to several meters is introduced by inaccuracies in visually placing each control point on the image. Four control points were common to both images, which helped ensure that the two images matched well in the overlapping areas. The locational accuracy of the rectification is unknown, and could not be determined without using much more accurate and expensive ground-based surveying techniques. However, the positional accuracy is probably within the range of 2 to 10 meters. This accuracy is more than adequate for the purposes of this project.

The two rectified images were mosaiced together using Erdas software. Very little displacement is present in the spliced region between the two images, indicating that the rectification process was internally consistent.

Image Classification

The images were classified with unsupervised, isodata classifier in Erdas to produce 27 statistically distinct spectral classes stored in a signature file. This signature file was then used to reclassify the raw image with a maximum-likelihood classifier. I examined each class from the resulting classification individually and visually compared each to the original photography to evaluate the correspondence of each spectral class to known ground features. This comparative procedure consists of flashing each of the classes on and off repeatedly while viewing the image on the screen, and simultaneously consulting the original photographs. The most distinctive classes had either very low

reflectance or very high reflectance in all three spectral bands. Extremely low reflectance values corresponded to tree crowns, the shadows cast by tree crowns, or standing water. Although appearing in the same spectral class, water was easily distinguished from tree crowns and shadows by pattern and texture. High reflectance values corresponded to bare sand patches, and human disturbances such as dirt roads and excavations. Naturally occurring bare sand patches were nearly always associated with xeric habitats, and had a distinctive, fine-grained pattern and texture compared to ground features created by humans. Spectral classes with intermediate reflectance were much more difficult to associate with ground features. In general, grass-dominated prairies, such as occur between scrub patches on N. Sandy Hill, had high reflectances that were only slightly less than bare sand. Areas dominated by oak shrubs were spectrally similar to areas containing various proportions of palmetto and wire grass. Discriminating among mixed shrub classes was difficult and also was believed unlikely to affect jay dispersion at APAFR. The dominant and most recognizable spectral classes corresponded to tree canopies and the shadows they cast, and bare sand patches. All spectral classes were recoded to the following landcover classes: 1 = tree cover, 2 = bare sand, 3 = mixed grass/shrub, 4 = wetlands/seeps. These classes were intended to reflect key structural components of the habitat rather than vegetative types.

Manual Editing of Classification

Manual editing of the final classification was necessary in some areas with very dark signatures that were confused with tree shadows. These areas of confusion were all wetlands or poorly drained areas with temporary standing water at the time the imagery

was acquired (March 1994). Most manual editing was accomplished using a single "mask" file, which contained wetland polygons digitized from the original rectified image. This mask file was used to recode all pixels inside of wetland polygons to the wetland category. Special attention was given to areas immediately surrounding jay territories. One cutthroat seep area adjacent to and just east of the NE territory (and experimental plot 1) on S. Sandy Hill showed standing water and trees. In this area, two dark pixel classes were found to have a good correspondence with tree cover, and two dark pixel classes corresponded with standing water. Theses classes were recoded accordingly.

Assessment of Classification Accuracy

Classification accuracy of percent tree cover was evaluated by comparison with estimates from line transect data collected at five control plots on S. Sandy Hill as part of the experimental manipulation experiment. A three pixel wide buffer was generated around each transect using Arc/Info. This buffer was used to sample the imagery around each transect using Erdas. Classification accuracy of bare sand was evaluated by comparison with estimates from quadrat samples (70 m across) collected on the northern section of S. Sandy Hill in areas largely devoid of pine trees. The measurements obtained from the imagery and the transect measurements were compared using a Paired T-Test and a correlation analysis.

Digitization of Territories and Background Features

Polygons representing the boundaries of jay territories and other background features (e.g. roads) were digitized directly off of the computer screen with a mouse from the mosaiced image using Arc/Info. This allowed the resulting coverages to be automatically georeferenced to the aerial photography

Tree Cover Buffering Procedure

GIS buffers were generated around each jay territory at 100, 200, and 400 m distances using Arc/Info. These buffers were used to characterize the habitat immediately surrounding each territory. A major complication with this procedure was that the buffers for each territory often overlapped with neighboring territories, and overlapping polygons are not allowed in Arc/Info coverages. Therefore, each territory was kept in a separate coverage and analyzed individually. The following procedure was used. Each coverage was buffered at distances of 100, 200, and 400 meters. The resulting coverages were converted to individual ERDAS ".dig" files. Each .dig file was overlaid on the classified image to calculate the percent tree cover within each buffer using an ERDAS program called POLYSTAT (developed by B. Stith and J. Richardson). The statistics generated from this program were imported into spreadsheet and statistical packages (Systat; SAS) for further analysis.

Habitat Quality Model

A habitat quality model was developed from the habitat variables using a habitat suitability index (HIS) approach similar to Duncan et al. (1995). The HSI model combines three HSI values for percent bare sand within territories (BS), percent tree cover within territories (TC), and distance to nearest forest (DF), to calculate a single habitat quality value (HQ) for each territory. The equation used for this model is

$$HQ = \sqrt[3]{BS * TC * DF}$$

The HSI values for each of the three habitat variables was obtained from step functions relating the habitat variable to an estimate of habitat quality (see Fig. 3-2 modified from Duncan et al. 1995). The shapes of these step functions were developed subjectively by D. Breininger. The habitat quality values were mapped automatically across the entire study area using the Spatial Modeler in the Imagine software package. The BS variable was mapped using the "focal sum" operator to count the number of bare sand pixels within 10 m of every point in the study area, and computing an HSI value using the function in Fig. 3-2a. The TC variable was similarly mapped by measuring tree pixels within a 60 m radius, and computing an HSI value using the function in Fig. 3-2b. To compute the DF variable, the TC layer was used and pixels surrounded by greater than 30% tree cover were coded as forest. The "search" operator was used to measure the distance to nearest forest for all pixels. The DF value was then computed using the function in Fig. 3-2c. The Imagine "summary" function was used to output HSI values

for each territory. Because "summary" requires integer values for input, the HSI values were resampled to 5 equal intervals.

Collection of Demographic Data

Demographic data for jays on Sandy Hill were collected by a team of field researchers (Brad Stith, Reed Bowman, Doug Stotz, Larry Riopelle, Natalie Hamel, and Mike McMillan) during 1994 – 1995, as part of a larger, on-going project that now monitors jays on the entire APAFR. All jays on Sandy Hill were captured, color-banded, and monitoried quarterly using techniques similar to Woolfenden and Fitzpatrick (1984). Nests were found and monitored during the spring and early summer. The raw demographic data are presented in Table 3 - 1.

Habitat-Demographic Analysis

I compared the demographic performance and habitat characteristics between the North and South Sandy Hill populations of jays. Owing to lack of normality for nearly all parameters (Table 3-2; Kolmorov-Smirnov test for normality), the nonparametric Mann-Whitney U statistic was used to test for demographic and habitat differences between the North and South study areas (Table 3-3).

I searched for habitat-demographic relationships by performing multiple linear regression (maximum R2 improvement technique for all combinations of variables) and logistic regression (SAS Institute). Demographic parameters served as dependent variables, and habitat measurements as independent variables.

Results

The locations and names of Florida Scrub-Jay territories throughout the study area are shown in Fig. 3-1. The division between the North and South population occurs at Kissimmee Rd. Note the absence of jays within the South population in the central part of S. Sandy Hill. This area has high densities of pine trees and little bare sand, and has three experimental plots where habitat restoration is underway.

A best-fit regression line, constrained to pass through the origin, showed a significant relationship between percent bare sand measured from quadrats vs. imagery (Fig. 3-4; r-squared = 0.60). The difference between the quadrat and image measurements was not significant (Paired T-test; mean difference = 0.9372, n=12, p=0.256), indicating no systematic bias in the measurements. Figure 3-5 shows the relationship between percent tree cover measured from transect data vs. imagery. A best-fit logarithmic regression line was drawn through the points (r-squared = 0.25). The differences between the transect and image measurements was not significant (Paired T-test; mean difference = 0.9372, n=40, p=0.824), indicating no systematic bias in the measurements. However, the large scatter of points deviated considerably from the expected distribution which would fall on a regression line intercepting the origin and having a slope of one. The logarithmic trend line suggested that the image measurements give higher than expected measurements at low tree cover values, and lower than expected measurements at high tree cover values.

Percent tree cover ranged from 4% to [illegible]% on S. Sandy Hill (Fig. 3-7), and only 0% to 4% on N. Sandy Hill (Fig. 3-6). The difference in tree cover between North and South was highly significant (Table 3 – 3; Mann-Whitney U Test, Z = -6.291, P <

0.0000). Most of the territories with high tree cover occured in the south end of S. Sandy Hill. Much greater variation was evident on S. Sandy Hill compared to N. Sandy Hill. Percent bare sand ranged from 9% to 30% on S. Sandy Hill, and 2% to 34% on N. Sandy Hill. The difference in bare sand cover between North and South was not significant (Table 3 – 3; Mann-Whitney U Test, $Z = -1.595$, $P = 0.111$).

Comparison of tree cover in North vs. South territories and in the three buffer zones (100, 200, and 400 m) showed striking differences (Fig. 3-8) and were highly significant for all comparisons. South territories showed a dramatic increase in tree cover with increasing distance from territories, while North territories showed only a slight increase. In the North, tree cover increased only slightly if at all as distance from territory increased (Fig. 3-9). In comparison, South territories showed large increases in tree cover as distance from territory increases (Fig. 3-10). A strong correlation was found between tree cover within territories and buffer zones in the South (e.g. r-squared = 0.88 for territories vs. 100m buffer), suggesting that these variables had strong spatial autocorrelation.

Comparison of tree cover within jay territories vs. total tree cover showed that jay territories have fewer trees than the area available to them for both the North and South territories (Fig. 3-11). Note that the measurements of available tree cover were made across the entire North and South study area rather than from subsamples, hence no standard deviations were calculated.

Measurements of bare sand within territories and the buffer zones showed a decreasing amount of bare sand away from territories for both the North and South territories (Figure 3-12), indicating selection of sandy areas by jays.

Comparison of demographic performance of jays in North vs. South for two years (1994, 1995) showed significant differences only for nonbreeder survival (Table 3 – 3; Mann-Whitney U Test, $Z = -2.396$, $P = 0.017$). Group size was nearly significant ($P = 0.060$). Number of fledglings produced, fledgling survival, yearling survival, and breeder survival were not significantly different.

Relationships between group size and percent tree cover within all territories (Fig. 3-13), and group size and percent tree cover within 100 m buffers (Fig. 3-14) showed decreasing group size with increasing tree cover. I lumped group size into 3 categories of roughly equal size and looked for differences in tree cover at the territory (Fig. 3-15) and 100 m buffer (Fig. 3-16). Large families (4 to 7 jays per group; $n = 13$) had lower median and variance in tree cover within and adjacent to their territories compared to medium (3 jays per group; $n = 7$) and small (2 jays per group; $n=15$) families. The differences, however, were not significant (Kruskal-Wallis one-way analysis of variance; tree cover $P = 0.205$; 100 m buffer $P = 0.186$). I lumped the 3 group categores into 2 group size categories (2-3 jays per group; 4-7 jays per group) and performed the same analysis, but the results were not significant.

Figures 3-17, 3-18, and 3-19 show side-by-side views of the classified and raw images for N. Sandy Hill, the N. portion of S. Sandy Hill, and the S. portion of S. Sandy Hill respectively. Jay territories are outlined in black. The names of jay territories are shown in Fig. 3-1. Three colors on the classified images correspond to tree cover (green), bare sand (white) and mixed shrubby or grassy vegetation (brown).

Figures 3-20 and 3-21 show presumed habitat quality as computed from the three HSI variables for the N. and S. portion of S. Sandy Hill respectively. High quality habitat

is shown in red (HSI = 0.81 - 1.0), medium quality habitat is shown in blue (HSI = 0.61 - 0.80), and low quality habitat is shown as white (HSI < 0.61). Jay territories (outlined in black) generally included substantial areas of low quality habitat in both the North and South areas.

I searched for correlations between demographic (fledglings, independent young, and yearlings produced, survival of fledglings, yearlings and breeders, and group size) versus the habitat variables (percent sand, percent tree cover within territories, percent tree cover within 100 m buffer, HSI for sand, HSI for distance to forest, HSI for trees within habitat, and combined HSI). The clearest bivariate patterns were for group size versus percent tree cover within territories (Fig. 3-13) and percent tree cover within the 100 m buffer (Fig. 3-14), but Kruskal-Wallis one-way analysis of variance results showed no significant differences between different group size comparisons and percent tree cover. Large group size variance existed in territories with low tree cover or adjacent to low tree cover, but there was a strong, nonsignificant trend towards smaller groups as tree cover increases. Kolmogorov-Smirnov tests for normality showed that bare sand was the only normally distributed habitat variable. Normality plots indicated that deviations from normality could not be corrected by commonly used (e.g. arcsine, inverse, log, square root) transformations. Nonparametric spearman rank correlation coefficients were low for all pairings of demographic and habitat variables. Multiple regression models never explained more than about 22% of the variation in demographic parameters using all combinations of habitat variables. Similarly, no habitat variables in several logistic regression models were significant.

Discussion

Accuracy of my remotely sensed habitat measurements is difficult to assess. Most remote sensing studies are conducted at a much coarser scale, and they attempt to identify discrete data classes (e.g. vegetation types). Such studies typically use a simple error matrix analysis where percent correct classification is given. I have little precedence to follow, since the goal of this classification was to provide continuous measurements (i.e. percent cover) from structural classes (e.g. tree cover or bare sand) rather than discrete vegetation classes. To assess the accuracy of these measurements quantitatively, I compared them to ground based measurements using paired T-Tests and simple correlation analysis. The bare sand measurements obtained from quadrats showed a fairly good correlation with the image measurements (Fig. 3-4). In contrast, the transect measurements of tree cover showed a weak correlation (Fig. 3-5). Some of these differences resulted from classification errors noticeable in comparisons of the photography with the classified image. Underestimates of tree cover were apparent in some of the young or very dense pine plantations, which tended to form a uniform canopy with few shadows. Overestimates were noted in areas with large scrub oaks, such as in some of the long unburned scrub patches on the W. side of N. Sandy Hill. Larger oaks spectrally may look very similar to pine trees. From a Florida Scrub-Jay standpoint, stands of large oaks may be as unusable as pine forests, so for modeling jay habitat it may be unnecessary to distinguish these tree cover types.

I suspect that many of the differences in tree cover estimates resulted from differences in the locations of transects measured on the ground vs. the image. Because transects are sampling vegetation intercepting a thin vertical plane, relatively small

difference in transect position can result in large differences in measurements. Quadrat measurements are probably less sensitive to positional inaccuracy than transects.

It was surprisingly difficult to estimate the magnitude of the positional inaccuracies of the transect locations. The locations of the transects were predetermined by a program that generated random locations for transect endpoints. These transect locations were plotted on high resolution photo maps which were taken into the field and used to stake out the transects. Thus, the correspondence between the GIS-based location and the actual ground location depended on the field person's ability to find the exact location from the photo map. My qualitative impression was that accuracy of positioning the transects depended on whether features visible on the photo map could be located on the ground. In sparsely forested areas, individual trees and bare sand patches were identifiable on the photo and ground, and served as good reference points. Under these conditions, a transect could probably be placed within several meters of its position on the photo. In heavily forested areas, good reference points were absent, and positional accuracy probably decreased, to errors of 10 meters or more. It might seem that differential GPS could solve this potential problem. Unfortunately, several factors make this approach more problematic than anticipated. First, the stated accuracy of the differential GPS approach available to us is 2 - 5 meters, which can misplace the ends of a transect by 3 pixels in any direction. Also, I have occasionally encountered averaged, differentially corrected points that are off by considerably more than 5 meters. Second, current GPS units often are unable to pick up the necessary signals within forests; precisely where they are most needed for this study. Third, the positional accuracy of the imagery itself is unknown, but is probably on the order of 2 to 10 meters (see

georeferencing section). Since there is no reason to expect errors in georeferencing to have the same bias as errors in GPS readings, the difference between the two could compound to exceed 15 meters. An error of this magnitude probably exceeds the expected error from a field person using a high resolution photo map to position a transect. Unfortunately, this leaves us with no way of quantifying and correcting positional inaccuracies. Recent advances in GPS technology may solve these problems as sub-meter accuracy becomes increasingly affordable and practical.

Quadrat samples and visual comparison of the classified image with the aerial photographs plus field knowledge suggest that the classification accurately reflected biologically important differences among habitats. The image processing techniques, combined with GIS files of the locations of jay territories and buffer zones, provided quantitative measurements of jay habitat in a quick and efficient manner. The quantitative results show dramatic differences in habitat structure between the North and South areas corresponding well to impressions reported by field researchers (R. Bowman pers. comm.). N. Sandy Hill jays have far fewer trees within and adjacent to their territories compared to S. Sandy Hill jays.

The image processing results confirmed our general field impressions about which jay families were living in good and poor quality habitat on Sandy Hill. Jays that occupied the poorest habitat were in the southern part of S. Sandy Hill. Here, several families were living in low quality habitat near a recent burn that was occupied by two or three other families. The presence of jays in poor habitat resulted from conspecific attraction (Smith and Peacock 1990) or "queueing" behavior, where individuals stay near high quality habitat to wait for breeding vacancies. Jays living in such poor habitat,

adjacent to good habitat, may create high variance in habitat-demographic relationships. Nevertheless, it is clear from the comparison of used versus available habitat that jays preferentially selected habitat with low tree cover (Fig. 3-11). These conditions exist throughout much of the N. Sandy Hill area, but on S. Sandy Hill they generally occurred only where recent fires were hot enough to kill most of the pines. These burns are embedded in a pine forest matrix (Fig. 3-9) presumably full of jay predators and competitors. In contrast, jays in N. Sandy Hill live in higher quality habitat embedded in a less hostile habitat matrix (Fig. 3-10). I suspect that these differences in tree cover explain the observed difference in nonbreeder survival between the North and South subpopulations.

In contrast to the observed difference in nonbreeder survival between the North and South subpopulations, and the nearly significant difference in group size, few clear relationships are obvious when pooling the two subpopulations and looking at individual territories. The locations of jay territories relative to the areas of highest habitat quality (Figs. 3-20 and 3-21) show that most jay territories included substantial areas of poor quality habitat. The scrub-jay model of Duncan et al. (1995) gave similar results; about 65% of their jay territories by area had HSI values below 0.5. Jay territories typically incorporate unusable habitat types simply because their territories are large in size relative to the patchiness of their habitat (Woolfenden and Fitzpatrick 1984). Both the North and South study areas are lacking in large, contiguous, high quality habitat patches. In the North, scrub patches occur on small lenses of well-drained soil surrounded by poorly drained soil. Scrub vegetation characteristic of high quality habitat can only grow on these well-drained soils. In the South, much larger areas of well-drained soil capable

of supporting high quality habitat are present, but high quality habitat occurs only in small areas that were recently burned or cleared experimentally. Five of 6 experimental plots were classified as relatively large patches of high quality habitat (see Fig. 3-21). Only plot 6 was not classified as high quality; for unknown reasons it had a dark reflectance when the area was photographed in March 1994. No jays have become established in the three isolated experimental plots (2, 3, and 4), despite their appearance as high quality. We suspect that conspecific attraction is extremely important to this species, greatly reducing the likelihood that solitary jays will become established in unoccupied, isolated patches.

The most important relationships I found for individual territories among the habitat-demography variables is a decline in group size with increasing tree cover, both within territories and within the 100 m buffer zones (Figs. 3-14 and 3-15). Large family sizes only occur in territories with low tree cover and adjacent to low tree cover. Variance in group size is high in the North because some groups accrue large size here, but not in the South. Territories in or adjacent to habitat with moderate to high tree cover have predictably small group sizes, presumably a result of successive years with poor productivity and low survival. A similar pattern between group size and tree cover can be seen in Figs. 3-16 and 3-17, where group size is lumped into 3 categories of roughly equal size.

Demographic parameters other than group size showed no clear patterns with the habitat variables at the individual territory level. Group size may be the least "noisy" measure of demographic success, since it integrates past and current demographic performance. Helper survival may be especially sensitive to habitat quality, since helpers

in poor quality habitat may have a greater tendency to emigrate than helpers in high quality habitat.

The remote sensing techniques described above show significant potential for evaluating Florida Scrub-Jay habitat. Tree cover and bare sand are important habitat variables that are relatively easy to measure with these techniques. Oak cover is likely to be important to scrub-jays, but the techniques I investigated could not discriminate oaks from other low-lying vegetation such as palmettos. Because of low mast failure and high acorn production, oak cover may not be a limiting factor for many scrub-jay populations. Further investigation of the importance of oak cover is needed.

The results of this study suggest that tree cover exceeding 20% - 30% within or adjacent to territories is associated with reduced demographic performance and may create "sink" populations of Florida Scrub-Jays. Although I lack direct evidence, much indirect evidence suggests that forest-dwelling predators and competitors explain the negative relationship between tree cover and demographic success. Sink populations can constitute a major proportion of a species population and may contribute to metapopulation longevity (Howe and Davis 1991), but the loss of a single critical source population may result in the extinction of all dependent sink populations (Pulliam 1988). Thus, management practices should seek to convert sink populations to self-sustaining source populations. The results of this study suggest that for the Florida Scrub-Jay, this entails keeping tree cover within and adjacent to jay territories at relatively low levels.

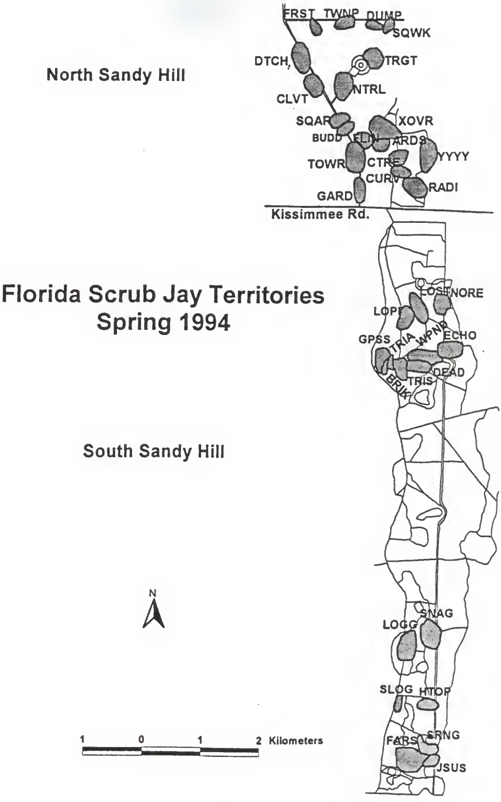


Fig. 3-1. Map of Scrub-Jay Territories - Spring 1994. Dividing line between "North" and "South" populations is the Kissimmee Rd..

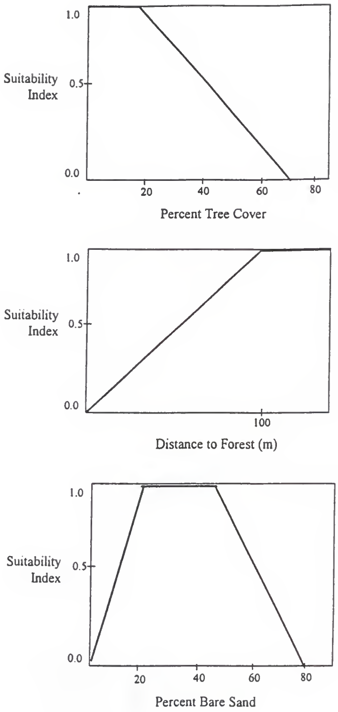


Fig. 3-2. Habitat Suitability Index graphs for percent bare sand, percent tree cover, and distance to forest (modified from Duncan et al. 1995).

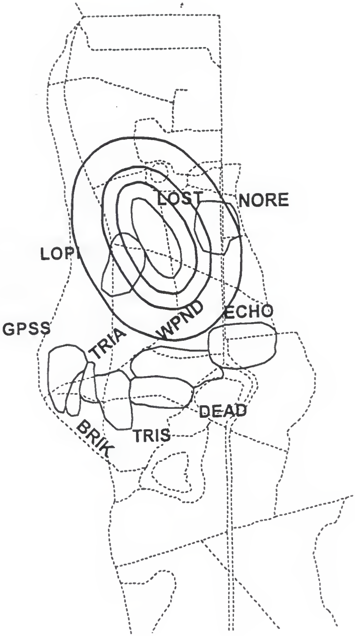


Fig. 3-3. Illustrative map of 100, 200, and 400 m buffer zones around LOST territory.

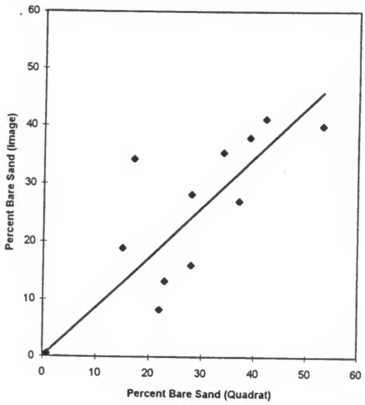


Fig. 3-4. Accuracy assessment correlation graph for bare sand based on quadrat vs. classified image measurements (r-squared = 0.60).

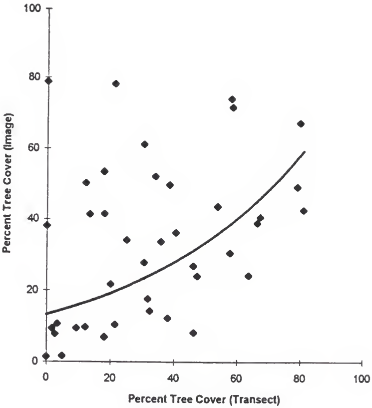


Fig. 3-5. Accuracy assessment correlation graph for tree cover based on transect vs. classified image measurements (r-squared = 0.25).

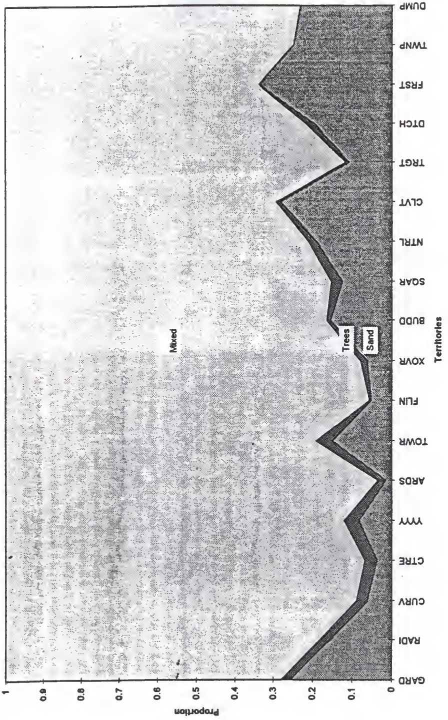


Fig. 3-6. Measurements of sand, tree cover, and mixed vegetation for Spring 1994 territories on N. Sandy Hill.

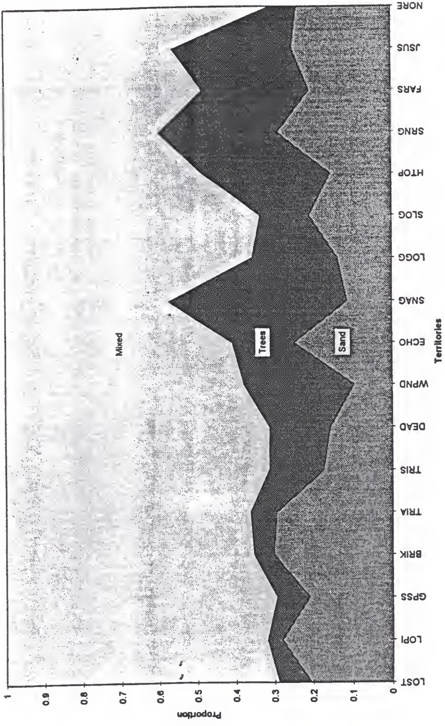


Fig. 3-7. Measurements of sand, tree cover, and mixed vegetation for Spring 1994 territories on S. Sandy Hill.

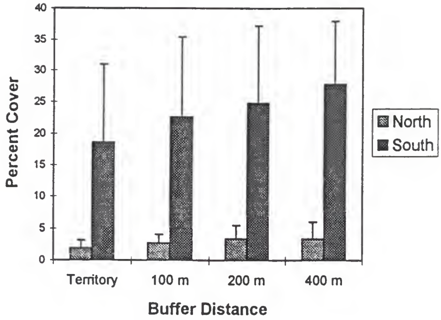


Fig. 3-8. Percent tree cover (mean and standard deviation) for 4 zones (inside territories, 100, 200, 400 m buffer) - North vs. South Sandy Hill. South population shows significantly higher tree cover within all zones compared to North population.

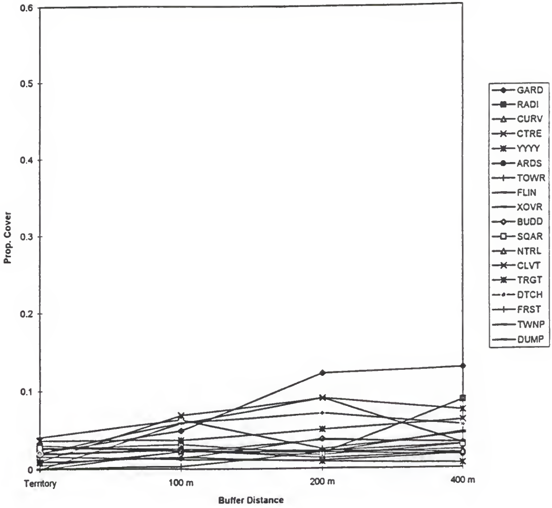


Fig. 3-9. Percent tree cover for individual territories for 4 zones (inside territories, 100, 200, 400 m buffer) - North territories.

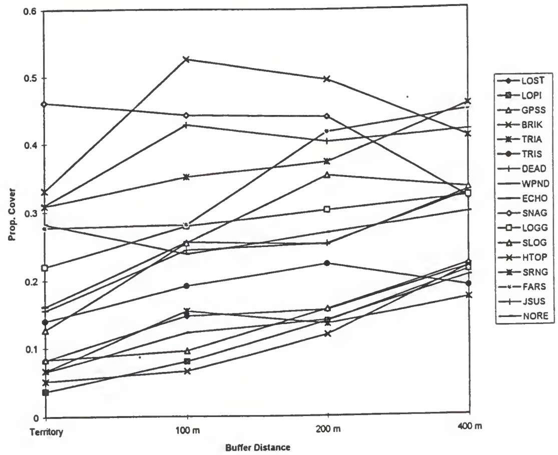


Fig. 3-10. Percent tree cover for individual territories for 4 zones (inside territories, 100, 200, 400 m buffer) - South territories.

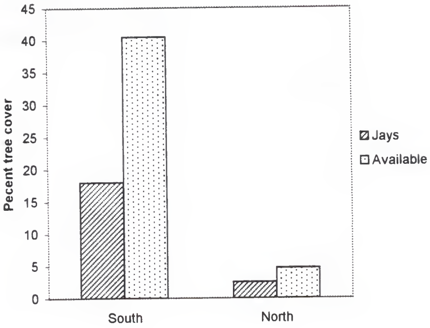


Fig. 3-11. Tree cover within jay territories vs. total tree cover in North vs. South Sandy Hill. Note that jays select habitat with lower tree cover in both areas.

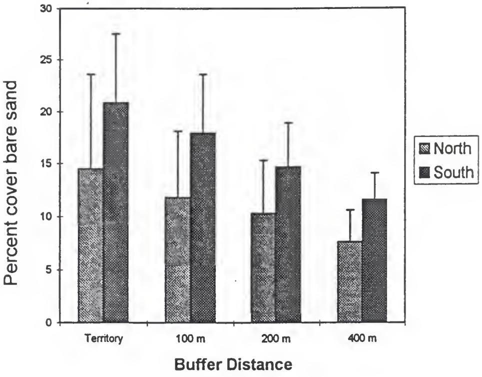


Fig. 3-12. Percent bare sand (mean and standard deviation) for 4 zones (inside territories, 100, 200, 400 m buffer) - North vs. South Sandy Hill. Differences between two areas are not significant.

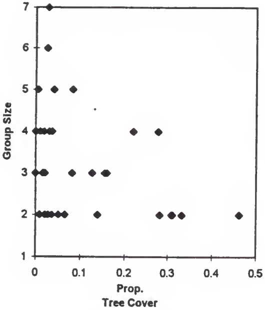


Fig. 3-13. Group size vs. percent tree cover within all territories (North and South populations pooled). Trend towards smaller group size with higher tree cover is not significant.

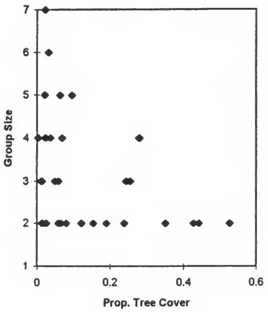


Fig. 3-14. Group size vs. percent tree cover within 100 m buffer for all territories (North and South populations pooled). Trend towards smaller group size with higher tree cover is not significant.

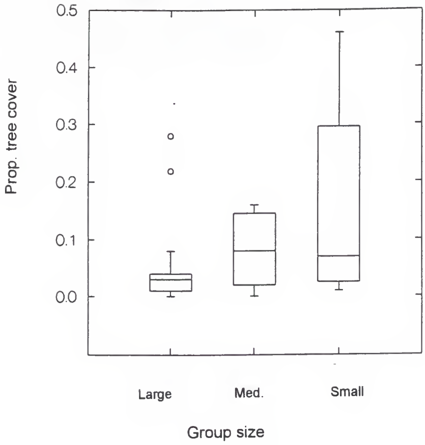


Fig. 3-15. Group size (small = 2, medium = 3, large = 4 – 7 jays) vs. percent tree cover within all territories (North and South populations pooled). Trend towards smaller group size with higher tree cover is not significant.

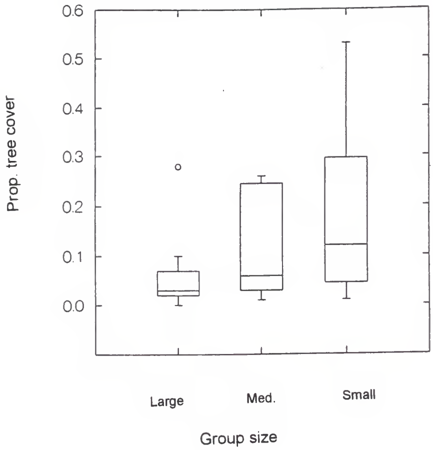


Fig. 3-16. Group size (small = 2, medium = 3, large = 4 – 7 jays) vs. percent tree cover within 100 m buffer (North and South populations pooled). Trend towards smaller group size with higher tree cover is not significant.

Fig. 3-17. Images and territories (black polygons) of North Sandy Hill. Right: color-infrared image. Left: classified image (white = bare sand; green = trees; brown = shrubs/grass; black = water).

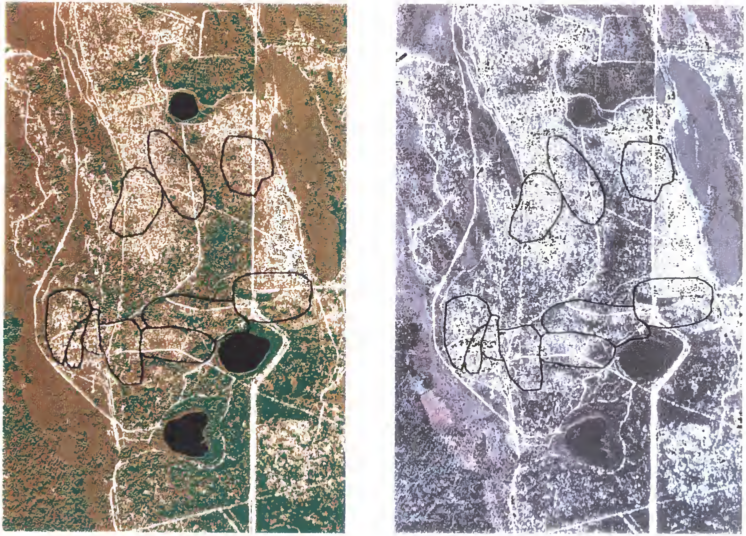


Fig. 3-18. Images and territories (black polygons) of N. portion of South Sandy Hill. Right: color-infrared image. Left: classified image (white = bare sand; green = trees; brown = shrubs/grass; black = water).

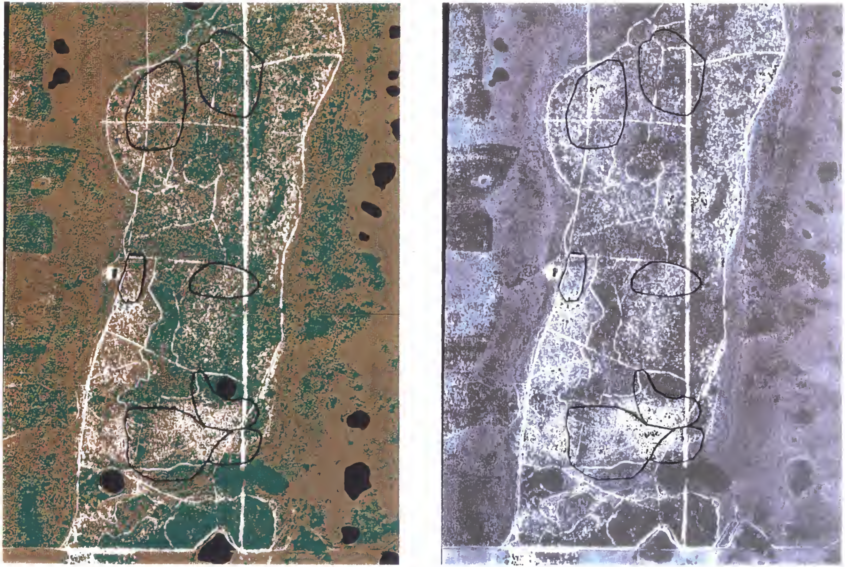


Fig. 3-19. Images and territories (black polygons) of S. portion of South Sandy Hill. Right: color-infrared image. Left: classified image (white = bare sand; green = trees; brown = shrubs/grass; black = water).

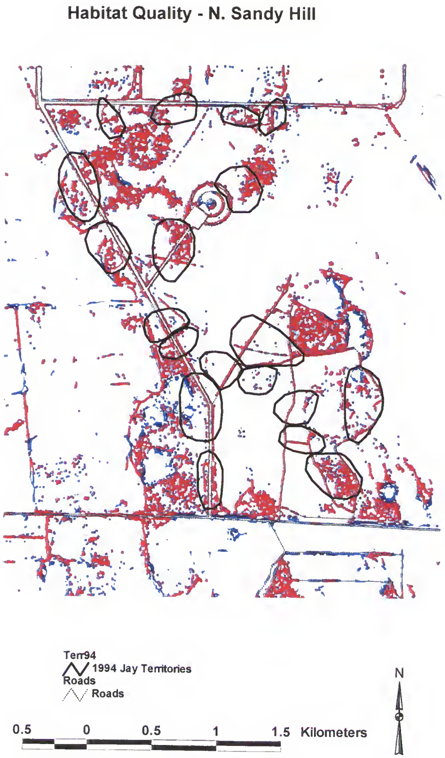


Fig. 3-20. Habitat quality map of N. portion of South Sandy Hill.

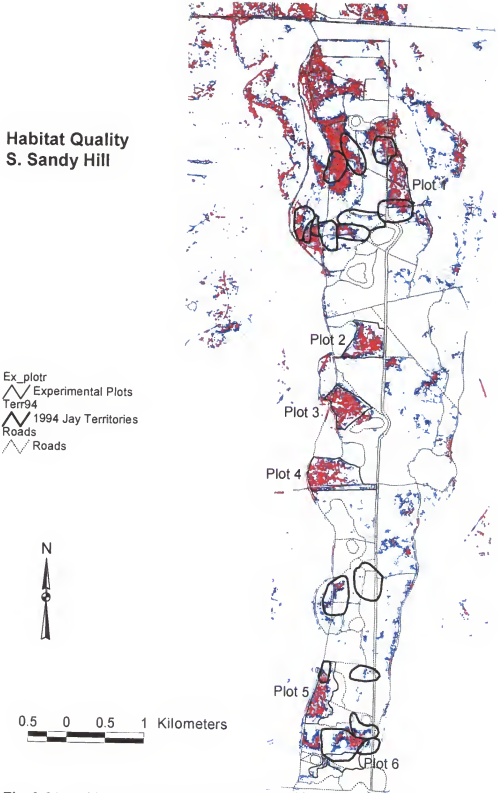


Fig. 3-21. Habitat quality map of S. portion of South Sandy Hill.

Table 3 – 1. Demographic and habitat parameters for North and South Sandy Hill (1994 – 1995).

Location	Territory	Year	Group Size	Fledgling Production	Yearling Production	Breeder Surv.	Helper Surv.	Fledgl. Surv.	Yearl. Surv.	Bare sand	Tree cover (inside territory)	Tree cover (100 m buffer)
NRIDGE	ARDS	1994	4	2	2	1	1	1	0	0.02	0.02	0.02
NRIDGE	BUDD	1994	2	2	2	0.5		1	0	0.15	0.01	0.01
NRIDGE	CLVT	1994	4	3	2	1	1	0.66	0	0.28	0.01	0.07
NRIDGE	CTRE	1994	4	2	0	0.5	0.5	0	0	0.04	0.03	0.02
NRIDGE	CURV	1994	2	4	1	0.5		0.25	0.25	0.16	0.03	0.03
NRIDGE	DTCH	1994	2	0	0	1				0.2	0.02	0.06
NRIDGE	DUMP	1994	3	0	0	1	1			0.23	0	0.06
NRIDGE	FLIN	1994	5	1	0	1	0.66	0	0	0.05	0	0.02
NRIDGE	FRST	1994	4	3	3	0.5	0.5	1	0.66	0.34	0	0
NRIDGE	GARD	1994	3	4	1	1	1	0.25	0	0.26	0.02	0.05
NRIDGE	NTRL	1994	2	2	1	1		0.5	0.5	0.19	0.02	0.02
NRIDGE	RADI	1994	6	0	0	0.5	0.33			0.16	0.03	0.03
NRIDGE	SQAR	1994	8	3	2	1	0.66	0.66	0	0.12	0.03	0.02
NRIDGE	TOWR	1994	5	4	3	0	0.66	0.75	0.25	0.15	0.04	0.06
NRIDGE	TRGT	1994	2	2	1	1		0.5	0	0.11	0.01	0.02
NRIDGE	TWNP	1994	4	3	3	1	0.5	1	0	0.25	0	0.02
NRIDGE	YYYY	1994	4	1	1	0.5	1	1	0	0.08	0.04	0.04
SRIDGE	BRIK	1994	2	4	3	0.5		0.75	0.25	0.3	0.05	0.07
SRIDGE	DEAD	1994	3	3	2	1	0	0.66	0	0.16	0.16	0.24
SRIDGE	ECHO	1994	3	0	0	1	0			0.25	0.16	0.26
SRIDGE	FARS	1994	4	5	3	1	0	0.6	0.2	0.21	0.28	0.28
SRIDGE	GPSS	1994	5	3	0	1	1	0	0	0.21	0.08	0.1
SRIDGE	HTOP	1994	2	3	2	0.5		0.66	0	0.15	0.33	0.53
SRIDGE	JSUS	1994	2	1	0	0.5		0	0	0.25	0.31	0.43

Table 3 – 1. Demographic and habitat parameters for North and South Sandy Hill (1994 – 1995).

Location	Territory	Year	Group Size	Fledgling Production	Yearling Production	Breeder Surv.	Helper Surv.	Fledgl. Surv.	Yearl. Surv.	Bare sand	Tree cover (inside territory)	Tree cover (100 m buffer)
NRIDGE	ARDS	1994	4	2	2	1	1	1	0	0.02	0.02	0.02
NRIDGE	BUDD	1994	2	2	2	0.5		1	0	0.15	0.01	0.01
NRIDGE	CLVT	1994	4	3	2	1	1	0.66	0	0.28	0.01	0.07
NRIDGE	CTRE	1994	4	2	0	0.5	0.5	0	0	0.04	0.03	0.02
NRIDGE	CURV	1994	2	4	1	0.5		0.25	0.25	0.16	0.03	0.03
NRIDGE	DTCH	1994	2	0	0	1				0.2	0.02	0.06
NRIDGE	DUMP	1994	3	0	0	1	1			0.23	0	0.06
NRIDGE	FLIN	1994	5	1	0	1	0.66	0	0	0.05	0	0.02
NRIDGE	FRST	1994	4	3	3	0.5	0.5	1	0.66	0.34	0	0
NRIDGE	GARD	1994	3	4	1	1	1	0.25	0	0.26	0.02	0.05
NRIDGE	NTRL	1994	2	2	1	1		0.5	0.5	0.19	0.02	0.02
NRIDGE	RADI	1994	6	0	0	0.5	0.33			0.16	0.03	0.03
NRIDGE	SQAR	1994	8	3	2	1	0.66	0.66	0	0.12	0.03	0.02
NRIDGE	TOWR	1994	5	4	3	0	0.66	0.75	0.25	0.15	0.04	0.06
NRIDGE	TRGT	1994	2	2	1	1		0.5	0	0.11	0.01	0.02
NRIDGE	TWNP	1994	4	3	3	1	0.5	1	0	0.25	0	0.02
NRIDGE	YYYY	1994	4	1	1	0.5	1	1	0	0.08	0.04	0.04
SRIDGE	BRIK	1994	2	4	3	0.5		0.75	0.25	0.3	0.05	0.07
SRIDGE	DEAD	1994	3	3	2	1	0	0.66	0	0.16	0.16	0.24
SRIDGE	ECHO	1994	3	0	0	1	0			0.25	0.16	0.26
SRIDGE	FARS	1994	4	5	3	1	0	0.6	0.2	0.21	0.28	0.28
SRIDGE	GPSS	1994	5	3	0	1	1	0	0	0.21	0.08	0.1
SRIDGE	HTOP	1994	2	3	2	0.5		0.66	0	0.15	0.33	0.53
SRIDGE	JSUS	1994	2	1	0	0.5		0	0	0.25	0.31	0.43

Table 3-1 – continued.

Location	Territory	Year	Group Size	Fledgling Production	Yearling Production	Breeder Surv.	Helper Surv.	Fledgl. Surv.	Yearl. Surv.	Bare sand	Tree cover (inside territory)	Tree cover (100 m buffer)
SRIDGE	LOGG	1994	4	0	0	0.5	0.5			0.14	0.22	0.28
SRIDGE	LOPI	1994	2	3	1	0		0.33	0.33	0.28	0.04	0.08
SRIDGE	LOST	1994	3	2	2	1	0	1	0	0.21	0.08	0.01
SRIDGE	NORE	1994	2	1	0	0.5		0	0	0.24	0.07	0.12
SRIDGE	SLOG	1994	3	0	0	0.5	0			0.21	0.13	0.25
SRIDGE	SNAG	1994	2	4	1	1		0.25	0	0.11	0.46	0.44
SRIDGE	SRNG	1994	2	4	1	1		0.25	0.25	0.29	0.31	0.35
SRIDGE	TRIS	1994	2	3	1	1		0.33	0.33	0.17	0.14	0.19
SRIDGE	WPND	1994	2	3	1	1		0.33	0	0.1	0.28	0.24
NRIDGE	ARDS	1995	5	3	0	0.5	0.33	0	0	0.01	0.02	0.02
NRIDGE	BUDD	1995	6	2	0	0.5	0.66	0	0	0.19	0.07	0.01
NRIDGE	DTCH	1995	2	3	0	1		0	0	0.23	0.01	0.01
NRIDGE	DUMP	1995	2	4	1	1		0.25	0	0.29	0.01	0.01
NRIDGE	FLIN	1995	2	1	1	0.5		1	0	0.09	0.03	0.01
NRIDGE	FRST	1995	5	0	0	1	0.66			0.24	0.04	0.02
NRIDGE	GARD	1995	4	2	0	0	0.5	0	0	0.32	0.09	0.06
NRIDGE	JUVI	1995	2	1	0	1		0	0	0.08	0.02	0.02
NRIDGE	NTRL	1995	3	3	1	0.5	1	0.33	0	0.26	0.01	0.01
NRIDGE	PURP	1995	2	3	0	0		0	0	0.1	0.02	0.02
NRIDGE	SQAR	1995	5	3	1	1	0.66	0.33	0	0.15	0.03	0.02
NRIDGE	TOWR	1995	5	3	1	0.5	0.66	0.33	0	0.21	0.01	0.04
NRIDGE	TRGT	1995	3	1	1	0.5	1	1	0	0.21	0.06	0.02
NRIDGE	TWNP	1995	6	2	2	1	0.33	1	0	0.16	0	0.02

Table 3-1 – continued.

Location	Territory	Year	Group Size	Fledgling Production	Yearling Production	Breeder Surv.	Helper Surv.	Fledgl. Surv.	Yearl. Surv.	Bare sand	Tree cover (inside territory)	Tree cover (100 m buffer)
NRIDGE	XOVR	1995	2	4	0	0		0	0	0.13	0.02	0.01
NRIDGE	YYYY	1995	5	0	0	0.5	0.66			0.07	0.06	0.05
SRIDGE	DEAD	1995	4	1	0	1	1	0	0	0.11	0.26	0.24
SRIDGE	ECHO	1995	2	0	0	1				0.28	0.17	0.18
SRIDGE	EXP5	1995	3	0	0	0.5	1			0.24	0.1	0.26
SRIDGE	FARS	1995	4	4	3	1	0	0.75	0.25	0.22	0.26	0.3
SRIDGE	GPSS	1995	5	0	0	0	0.33			0.32	0.01	0.05
SRIDGE	HTOP	1995	4	0	0	0	0			0.13	0.36	0.48
SRIDGE	JSUS	1995	2	4	2	1		0.5	0	0.09	0.53	0.55
SRIDGE	LOGG	1995	2	0	0	0	0			0.16	0.18	0.21
SRIDGE	LOPI	1995	4	0	0	0.5	0.5			0.26	0.07	0.1
SRIDGE	LOST	1995	3	0	0	1	0			0.17	0.14	0.17
SRIDGE	NORW	1995	3	1	0	0.5	1	0	0	0.21	0.03	0.03
SRIDGE	SNAG	1995	4	1	1	0	0.5	1	0	0.14	0.48	0.45
SRIDGE	SRNG	1995	3	3	0	1	1	0	0	0.25	0.33	0.37
SRIDGE	TRIS	1995	3	1	1	1	1	1	0	0.21	0.08	0.12
SRIDGE	WPND	1995	3	3	2	0.5	0	0.66	0	0.13	0.23	0.29

Table 3 – 3. Mann-Whitney_U test for differences in demographic and habitat variables between North and South jay populations (* significantly).

	Group size	Fledgling production	Yearling production	Breeder survival	Nonbreeder survival	Fledgling survival	Yearling survival	Bare sand	Tree cover (inside territory)	Tree cover (100 m buffer)
Mann-Whitney_U	376.500	453.500	480.500	508.000	127.500	286.500	257.000	393.000	50.000	45.000
Z	-1.881	-.798	-.446	-.052	-2.396	-.155	-1.063	-1.595	-6.219	-6.308
P-value	.060	.425	.655	.959	.017*	.877	.288	.111	.000*	.000*

CHAPTER 4
MODELING DISPERSAL IN THE FLORIDA SCRUB-JAY

Introduction

Dispersal is a fundamental biological process of great importance to many fields of biology, including population biology, population genetics, behavioral ecology, and conservation. Understanding dispersal is becoming increasingly important in conservation biology, as dispersal ability may determine whether a given species can survive in the face of ever-increasing habitat fragmentation. Spatially explicit population models (SEPM) provide a formal framework for investigating the importance of dispersal to the viability of populations within a given landscape. The use of SEPMs in conservation is growing rapidly (Beissinger and Westfal 1998). Yet, little is known about dispersal for most species, leading some to question the value of predictions obtained from SEPMs. Thus, the quality of dispersal data and its use in population modeling was a key issue in an important court case involving the Federally threatened Northern Spotted Owl (Harrison, Stahl, and Doak 1993). More recently, Winnergren et al. (1995) and Ruckelhaus et al. (1997) developed a simple dispersal model that was extremely sensitive to relatively small differences in estimates of dispersal mortality. They argued that dispersal data would never be known with enough accuracy to be used reliably in SEPMs. In response to these criticisms, Mooij and DeAngelis (1999) and South (1999) developed alternative simple models showing SEPMs to be relatively

insensitive to errors in dispersal parameters except under very limited conditions. The debate over the reliability of SEPMs is likely to continue, but as South (1999) points out, model sensitivity to dispersal parameters may be greatly reduced by increasing model realism.

The Florida Scrub-Jay offers an excellent opportunity to develop an extremely realistic SEPM. Extensive dispersal information is available for this intensively studied species (e.g. Woolfenden and Fitzpatrick 1984). Furthermore, there is great concern for this species, which is listed as a threatened species Federally and by the State of Florida. Much is known about the spatial distribution of the species (e.g. chapter 2), making it feasible to model the entire population. Root (1996, 1998) used RAMAS GIS to develop the first SEPM for scrub-jays. Root's research was focused on four somewhat isolated populations within Brevard county, Florida. She modeled dispersal among these four populations for female jays only, using the interpatch distances and the ABS dispersal curve to estimate migration rates. Her results suggested that interpatch dispersal was important for offsetting the deleterious effects of epidemics. Root (1998) stated that her estimates of dispersal likely were optimistic and suggested that a better approach would account for differential dispersal rates based on the interpatch matrix.

In this chapter I describe a SEPM I developed to account for the influence of interpatch matrix on dispersal, as well as a host of other biological details documented in the extensive scrub-jay literature (see Woolfenden and Fitzpatrick 1996 for a recent literature review). The SEPM is an individual-based model; it tracks all individuals of both sexes from birth to death, and simulates the daily movement of individuals during dispersal within and between habitat patches.

Individual-based models are appealing because they allow the inclusion of almost any biological detail, giving them unrivaled realism (Huston et al. 1988; Judson 1994). Because they often incorporate behavioral mechanisms, the parameters in an individual-based model tend to have clear biological meaning and typically are directly measurable in the field. The increased level of detail inherent in an individual-based model also provides more opportunities to compare model output with different types of field data for validation purposes. Finally, the increased realism of individual-based models makes them more likely to reveal dynamics that would otherwise be missed in a less detailed model.

Individual-based models have been developed for a few avian species, including Bachman Sparrow (Pulliam et al. 1992), Northern Spotted Owl (McKelvey et al. 1993), American Wood Stork (Wolff 1994), Helmeted Honey Eater (McCarthy 1996), and Red-cockaded Woodpecker (Letcher et al. 1998). The excellent field data and well-known behavioral characteristics of the Florida Scrub-Jay make this species an excellent candidate for an individual-based modeling approach.

The overall objectives of this chapter are as follows:

- Develop a set of algorithms and parameters specifically for the Florida Scrub-Jay to simulate dispersal in an individual-based model.
- Calibrate the dispersal module using long term field data from Archbold Biological Station data, and radiotelemetry data acquired from a displace-and-release experiment.

- Validate the dispersal module by comparing model output to Archbold Biological Station dispersal and stage-age data.
- Use constraint analysis to place plausible bounds on long distance dispersal parameters. Using a realistic digital landscape for which dispersal data is available, develop parameters that result in simulated dispersals between patches with known exchanges, and no simulated dispersals between patches with no observed exchanges.

Dispersal Strategies

The ornithological literature generally recognizes two extreme dispersal strategies: "delay and foray" versus "depart and float". The "floater" strategy, wherein nonbreeders depart from their natal territory and wander in search of mates or unoccupied habitat with little or no tendency to return to the natal territory, is common among non-cooperative breeding birds (Zack 1990). From an optimal foraging standpoint, to move through poor habitat efficiently floaters should travel in a fairly linear fashion, moving with a low turning rate, weak turn bias, and strong locomotory rate (Bell 1992; Turchin 1998). Such straight line movements by floaters have been observed for Red-Cockaded Woodpeckers (Letcher et al. 1998) and a variety of other organisms (Zollner and Lima 1999). This linear movement allows floaters to quickly leave unproductive areas. Once good habitat or potential mates are encountered, a floater should move in a manner that keeps it within that patch by moving with a high turning rate, strong turn bias, and small movements (Bell 1992; Turchin 1998). This type of localized searching behavior is also exhibited by "delay and foray" dispersers, who engage in temporary "dispersal forays" away from their natal territories in search of breeder vacancies (Woolfenden and

Fizpatrick 1984). Because such forays usually are unsuccessful and end with a return to the natal territory, the territories visited tend to fall within an "assessment sphere" around the natal territory. When a successful dispersal occurs, the resulting dispersal distances will be smaller on average than for floaters (Zack 1990).

Dispersal Traits of the Florida and Western Scrub-Jay

The floater and delay-and-foray dispersal strategies are well illustrated by the contrasting behavior of Florida and Western Scrub-Jays. Formerly considered a subspecies of the Western Scrub-Jay, the Florida Scrub-Jay was recently given full species status (Woolfenden and Fitzpatrick 1996). The Florida Scrub-Jay is likely descended from jays that colonized Florida from western North America during the Pleistocene, perhaps as recently as 4 million years ago (Woolfenden and Fitzpatrick 1996). Subsequent isolation of jays in Florida from the western population resulted in the evolution of significant genetic and behavioral differences (Woolfenden and Fitzpatrick 1996). Some of the most striking differences between the two species relate to dispersal behavior, a fact which makes comparison of the two species helpful in developing a model of dispersal behavior.

Several lines of evidence suggest that Florida Scrub-Jays "saturate" high quality habitat, and do not occupy marginal habitat because survival and reproduction is poor (Woolfenden and Fitzpatrick 1984; Fitzpatrick and Woolfenden 1986). To survive, young Florida Scrub-Jays must occupy high quality habitat. But Florida Scrub-Jays are highly territorial and vigorously chase away non-resident jays; dispersers cannot easily move through occupied habitat. Instead, they employ a "delay and foray" strategy, wherein they make short forays to investigate nearby breeder vacancies or unoccupied habitat, and

retreat to their natal territory when chased by resident breeders. By contrast, the floater strategy prevails in Western Scrub-Jays in part owing to breeder tolerance of nonbreeders in their territory (except briefly at the beginning of breeding season; Carmen 1989; Koenig et al. 1992). This option of floating among breeders in high quality habitat is unavailable to Florida Scrub-Jays because breeders are largely intolerant of floaters. Thus, as floaters Florida Scrub-Jays would be forced to reside in marginal habitat where they would suffer high predation rates as documented in Fitzpatrick and Woolfenden (1986). Western Scrub-Jays also have an advantage here, since their survival rates in marginal habitat are nearly the same as in high quality habitat (Carmen 1989; Koenig et al. 1992).

The above considerations are nicely encapsulated by Fitzpatrick and Woolfenden (1986) in an evolutionary model of dispersal for the genus *Aphelocoma.* Their model suggests that selection will favor individuals who attempt to breed immediately upon maturation, rather than delaying dispersal, unless the cost of dispersal is high compared to the cost of remaining home and not breeding. Delaying dispersal, foregoing early breeding opportunities, and engaging in low risk forays are the predominant dispersal behavior for Florida Scrub-Jays in natural, high quality habitat. Nevertheless, documented cases of long distance dispersal by some Florida Scrub-Jays make it clear that they sometimes engage in risky dispersal behavior by moving through "matrix" habitat between high quality habitat patches. Such behavior, though not completely analogous to Western Scrub-Jay dispersal, can be modeled as floater dispersal behavior. These considerations suggest that a reasonable approach to modeling dispersal in the

Florida Scrub-Jay is to simulate both types of dispersal behavior (i.e., delay-and-foray and float).

Methods

General Approach

I simulated dispersal in the Florida Scrub-Jay with two distinct algorithms, one for jays that engage in short forays away from their natal territory ("philopatric" algorithm), another for jays that become floaters and move long distances from their natal territory ("floater" algorithm). The philopatric dispersal algorithm is intended, 1) to simulate the prevalent mode of dispersal observed in real jay populations, 2) to produce the majority of dispersals within a given simulation, and 3) to produce the modal distribution of dispersal distances in simulated populations. The philopatric algorithm produces no dispersals beyond a specified radius referred to as the "assessment sphere". The floater algorithm completely determines the tail of the distribution, as philopatric jays settle only within the radius of the assessment sphere. Together, the two algorithms produce the combined dispersal curve; the philopatric algorithm produces dispersals ranging from the natal territory (i.e. inheritance) out to the radius of the assessment sphere, the floater algorithm produces dispersals beyond the assessment sphere.

Considerable information from long term, color band studies (e.g. Woolfenden and Fitzpatrick 1984) is available to aid in the simulation of philopatric dispersal. In contrast, much less is known about jays that disperse as floaters. Although some long distance dispersals have been documented, the number of observed movements is small

(< 20 birds from Archbold Biological Station; John W. Fitzpatrick, pers. comm.), and the movement and behavior of such jays remains essentially unobserved. To acquire some empirical data on floaters, a small radiotelemetry study was conducted for this dissertation.

GIS Files

The GIS files used in the simulations for this chapter and chapter 5 were created by overlaying the scrub patches obtained during the 1991-1992 statewide Florida Scrub-Jay survey (see chapter 2) onto a statewide habitat classification map produced by the Florida Game and Freshwater Fish Commission (FGFWFC) in 1992 (Kautz et al. 1993). Spatial resolution of the GIS file was 30 m. The original landcover types coded in the FGFWFC classification are shown in Table 4-1.

Simulating Philopatric Dispersal

I modeled the behavior of helpers searching for breeding vacancies near their natal territory using a small set of behavioral rules. Helpers engaged in philopatric dispersal are assumed to have perfect knowledge of the status of each territory within their assessment sphere. Helpers compete for vacancies; older helpers out compete younger helpers, and closer helpers out compete more distant helpers. Dispersers that find no vacancies during this search return to their natal territory and remain as helpers until the following year.

Philopatric disperser survival rate is not directly specified in the model, but is related to the floater frequency rate described below.

Short distance dispersal algorithm development and calibration

To develop and calibrate the model I relied heavily on dispersal and stage-age data obtained from Archbold Biological Station (raw data provided by J. Fitzpatrick and G. Woolfenden). Because dispersal curves are highly sensitive to the spatial configuration of territories, comparisons between Archbold data and model output were made by running simulations that approximated the dispersion of territories and habitat in the vicinity of Archbold Biological Station. These simulations included approximately 200 territories and encompassed the southern third of Highlands county, and parts of Desoto and Glades counties.

Development and calibration of the model proceeded by iteratively running a simulation of the Archbold scenario, comparing the resulting dispersal and stage-age graphs with the Archbold data (see Figs. 4-4 through 4-7), then modifying the model structure or parameter values to improve the fit between the model and field data. Initial modeling attempts that used very simple algorithms failed to match the Archbold data. An early implementation used the following simple rule: allow randomly selected helpers to occupy randomly selected territories within their assessment sphere. Dispersal behavior was modified by adding rules that altered the manner in which dispersers departed, moved, and settled in new locations. Rules were added to the model only if they made biological sense and increased the realism of the model. I relied heavily on Woolfenden and Fitzpatrick (1984) for behavioral information that could be incorporated into the model. The final set of rules is provided in Table 4-2. The two sexes were treated differently to account for observed, sex-based differences in dominance, natal inheritance, and dispersal behavior.

Simulating Long Distance Dispersal

Searching behavior of long distance dispersers is modeled with several simple rules that are hardcoded into the module. The initial movement direction upon leaving the natal territory is random. As dispersers move through the landscape, they see territories or habitat within a user-specified detection radius. They process the objects they see in a specific order: first breeder vacancies, then empty territories, and finally, habitat. When a breeder vacancy or empty territory is detected, the decision to settle is determined by the disperser's propensity to settle (set by the user – default is always to settle). If the disperser doesn't settle, it moves on towards the most attractive habitat that has not been visited already. Dispersers move in a straight line only within homogenous habitat, and deviate from a straight line when they detect a difference in habitat attractiveness (see section below). They avoid habitat with low attractiveness, and move towards habitat with high attractiveness. Dispersers remember previously visited locations, which makes it less likely that they will backtrack unless alternative directions are very unattractive.

Values for several floater parameters can be modified, including the proportion of helpers that become floaters, detection radius (maximum distance objects can be detected), mobility (maximum daily distance moved), and daily survival. For some parameters (mobility, mortality, floater formation), estimates could be derived from empirical data; indirect methods were used for directionality and estimation of detection radius.

Estimating floater mortality and mobility

Long distance dispersers have two daily survival rates: one for floaters within scrub, another for floaters outside of scrub. Within scrub, the daily survival rate is assumed to be higher than outside of scrub, and similar to survival rates of nondispersing jays of similar age and same sex. The survival rate for dispersers outside of scrub is drawn from the "best-guess" Kaplan-Meier curve (Fig. 4-2) derived from the displacement experiment described below. This curve was hard-coded into the model and daily survival rates were drawn from the distribution and applied to floaters moving in the matrix between scrub patches. An option to use a constant daily survival rate (as in scrub habitat) was also included in the model and evaluated in the constraint analysis.

Each disperser moves until it exceeds a daily-distance-moved threshold value selected for each jay from a function that approximates the observed distribution of daily move distances. This distribution was derived from field data obtained from the displacement experiment described below. The function that approximates the field distribution was generated by the curve fitting procedure of SPSS (ver. 7.5). The distribution of distances excluded 0 distances (i.e. days when jays did not move - see later discussion on displacement experiment). Once the daily-distance-moved threshold is exceeded, each jay's daily mortality rate is used to determine if the jay survives to the next day. These steps are repeated until each jay dies, finds a mate or vacant territory, or leaves the simulation area. The order in which dispersers move is randomized each time all jays have taken a step. Jays that leave the area are considered dead (i.e. there is no immigration from outside the simulation area). In contrast to short distant dispersers, long distance dispersers do not return home.

Habitat attractiveness

Five attractiveness values are used in the model: 0 for a repulsive landcover that jays do not enter, 1 for an unattractive landcover, 2 for a neutral landcover, 3 for a somewhat attractive landcover, and 4 for a highly attractive landcover. The attractiveness values assigned to different landcover classes in the GIS files (described in the previous GIS section) are provided in table 4-1.

Floater detection radius

The floater detection radius is the maximum distance at which a disperser can be expected to detect another jay or vacant territory. A starting point for estimating this parameter is the distance between tape playback census points, as recommended by Fitzpatrick et al. (1991b p. 13): "Adequate spacing between transects can be estimated roughly as the distance at which a person listening to the tape directly in front of the speaker perceives the "bird" to be no more than about 100 meters away. A distance of 100 to 200 meters between transects and between stations is generally adequate when using a good-quality, hand-held cassette player broadcasting at full volume." Jays no doubt see each other, especially during territorial display flights, at greater distances than they can hear each other. A value of 450 meters was selected as the default value for the detection radius.

Estimating floater frequency

For most bird species, all surviving young depart from their natal territory as floaters upon reaching sexual maturity, often during the first year of life. From a modeling standpoint, the proportion of young that become floaters is simply the proportion that survive to dispersal age. Upon reaching dispersal age, all young "disappear" permanently from their natal territory and become floaters searching for breeder vacancies or unoccupied habitat. For Florida Scrub-Jays and other species that delay dispersal, the situation is more difficult to model, as some dispersal age young may return to their natal territory after making unsuccessful searches for nearby breeder vacancies, while other young may depart permanently from their natal territory.

The objective of this section is to estimate the annual proportion of helpers that become floaters ($D_{floater}$). The dispersal model uses $D_{floater}$ to establish the proportion of jays that become floaters from the pool of jays that disappear. The starting point for estimating $D_{floater}$ is D_{total}, the total proportion of helpers that disappear annually. All floaters must come from this pool of disappearing jays, so $D_{floater}$ must be less than or equal to D_{total}. D_{total} is calculated from field data as the number of helpers disappearing during a year divided by the original number present at the start of the year. D_{total} for helpers is shown in Table 4-2 (taken from appendix M of Woolfenden and Fitzpatrick 1984).

From the modeling standpoint, D_{total} has two components: jays that disappear by dying locally (i.e. within their assessment sphere), and jays that "disappear" by becoming floaters who move beyond their assessment sphere and either die or become breeders. This can be represented as equation 4-1:

$$D_{floater} = D_{total} - D_{local} \qquad \text{(Eq. 4-1)}$$

Thus, the proportion of helpers that disappear and become floaters ($D_{floater}$) is equal to the total proportion of helpers observed to disappear (D_{total}) corrected downward by subtracting the proportion of helpers expected to die locally (D_{local}) within their assessment sphere. Because D_{total} varies among sex and age class, to facilitate setting and comparing these parameters we can normalize the values relative to D_{total} and designate the new parameters with the prefix "P". Thus, $P_{floater} = D_{floater} / D_{total}$, and normalizing equation 4-1 we get:

$$P_{floater} = D_{total} / D_{total} - D_{local} / D_{total} = 1 - P_{local} \qquad \text{(Eq. 4-2)}$$

where $P_{floater}$ is the proportion of total disappearances due to floaters permanently leaving their natal territory, and P_{local} is the proportion of total disappearances due to local death within the assessment sphere. Note that the floater disappearance rate ($P_{floater}$) determines how many helpers disperse beyond their assessment sphere, but does not determine how many floaters survive to become breeders. The fate of floaters (i.e. whether they die or become breeders) is contingent on the runtime situation and landscape encountered by floaters during simulations as they search for breeder vacancies.

The sum of $P_{floater}$ and P_{local} must equal 1 (equation 4-2), so setting the value of one parameter completely determines the other. I know of no way to directly estimate $P_{floater}$ and P_{local}. However, it is possible to set reasonable bounds on these parameters by considering various aspects of Florida Scrub-Jay biology.

For example, Waser et al. (1994) describe a flexible approach for estimating from census data the proportion of unobserved emigrants that survive, based on several types of data such as the known number of successful immigrants, and the known survival rates of non-dispersing sex and age classes. They cite Woolfenden and Fitzpatrick (1984) as the earliest example of such an approach. Woolfenden and Fitzpatrick (1984 appendix M) estimated the number of dispersers expected to successfully emigrate off their study area and subtracted these estimates from the known disappearances to calculate more accurate helper mortality rates. Their approach assumes that immigration and emigration are at equilibrium. Table 4-2 shows their "equilibrium" mortality rates (column labeled D_{eq}) next to the total disappearance rates (D_{total}). The difference between D_{total} and D_{eq} ($E_{nonlocal}$ in table 4-2) is the proportion of disappearing helpers expected to become breeders off the study area. If we assume that this emigration rate ($E_{nonlocal}$) is the proportion of disappearing helpers that successfully became breeders by dispersing as floaters, we can use $E_{nonlocal}$ as a lower bound for $P_{floater}$. That is, the proportion of disappearing helpers becoming floaters must be at least as big as the proportion of helpers that successfully emigrate off the study area. Thus, $E_{nonlocal}/D_{total}$, which is the proportion of disappearing jays estimated to became breeders off Archbold Biological Station, establishes a lower bound for $P_{floater}$, and because the proportion of floaters that die is likely to be very high, $P_{floater}$ is likely to be much greater than $E_{nonlocal}/D_{total}$.

We can develop an upper bound for $P_{floater}$ by using the fact that the sum of $P_{floater}$ and P_{local} must equal 1 (equation 4-2) and estimating P_{local}, the proportion of disappearances due to local death rather than floating. We begin with the assumption that jays engaged in local forays are likely to die at the same or higher rate than jays of similar

age or experience who are not making frequent forays away from their natal territory (i.e. breeders or older fledglings). As an example, consider yearling helpers that disappeared at Archbold Biological Station (D_{total} female = 0.42, male = 0.22; table 4-2). The local death rate of yearling helpers is almost certainly greater than that of breeders (0.18; Woolfenden and Fitzpatrick 1984, table 9.2, p. 265), but may be lower than the death rate of older fledglings (0.30; Woolfenden and Fitzpatrick 1984, fig. 9.1, p. 255). If we assume that P_{local} is less than 0.30, suppose 0.25, then the maximum value for $P_{floater}$ would be 0.75 ($P_{floater}$ must be less than (1 - P_{local}); eqn. 4-2).

In the real world, the proportion of helpers that become floaters may vary greatly, depending on factors such as habitat quality or number of neighboring territories. Some of these factors are reviewed below in the discussion. If we consider the Archbold setting, for yearling male helpers, it is likely that most disappearances can be attributed to local mortality within their assessment sphere, while the proportion of females dying within their assessment sphere may be less because more females disperse as floaters. However, since the female assessment sphere is larger than the male, the proportion of females dying within their assessment sphere may be substantial. Furthermore, 2nd year males are estimated to have the largest proportion of disappearances due to emigration (Table 4-2; column $E_{nonlocal}$/ D_{total}), suggesting that $P_{floater}$ also might be considerable for older male helpers.

Since the disappearance rates (D_{total}) of female helpers are considerably greater than males, setting $P_{floater}$ equivalent for both sexes would produce substantially more female than male floaters. The values for $P_{floater}$ likely are larger for females than males, which further increases this bias in the number of female floaters. Although it may seem

that producing larger numbers of female floaters may inflate female survival rates because many may survive if they find vacancies outside the assessment sphere, recall that disappearance rates (D_{total}) for females are substantially higher than males, so more female floaters must survive to achieve the equilibrium rate (D_{eq} in Table 4-2).

Based on the above considerations, upper and lower bounds for $P_{floater}$ are listed in Table 4-2, along with a "best guess.". The sensitivity of the model to different $P_{floater}$ settings likely will vary considerably with the configuration of the landscape, and will be investigated at a later time. A constraint analysis was performed to assess model sensitivity for the Archbold setting as described in a section below.

Floater algorithm development and calibration

Whereas a wealth of biological data is available to aid in the simulation of short distance dispersal, much less is known about long distance dispersal. A few long distance dispersals by Archbold birds have been documented during comprehensive off-station surveys for color-banded birds, but these established birds provided little information about the process by which they moved and became established. Radiotelemetry offers the best hope for documenting the movement and interactions of long distance dispersers, but such studies face serious logistic difficulties (Koenig et al. 1996). Foremost among these is the low likelihood of tagging a reasonable number of jays that then become long distance dispersers. Most birds will disperse a short distance, yielding little or no information useful for modeling long distance dispersal. By knowing the sex, age, and dominance of birds within a study area, the likelihood of tagging long distance dispersers might be increased, but even then most of the prime candidates for dispersal will move only a small distance. A further complication for the present study is that transmitters

appropriate for Florida Scrub-Jays currently have a battery life of only a few months, necessitating frequent recapture and re-outfitting. An alternative approach to waiting for jays to disperse is to artificially displace radiotagged jays and follow their movement and survival.

Jay displacement experiment

Displacement experiments have a long history within ornithology, having been conducted in numerous studies of homing ability (Papi 1992). The focus of my displacement experiment was not homing ability, but to induce birds to make long distance movements that might mimic natural movements of jays moving between isolated scrub patches in different landscape matrices. Surprisingly, the application of this technique in conservation biology to date is extremely rare.

Jay selection protocol. Owing to large differences among sexes and stages in documented dispersal distances, I selected the sex and stage having the best chance of dispersing long distances, viz. females rather than males, and experienced helpers rather than breeders or juveniles (one exception was a female breeder taken from Orange County in a mitigation deal). Jays of known sex and stage were selected for capture from the color-banded population from the "experimental tract" of Archbold Biological Station (then maintained and monitored by Ron Mumme). A total of 10 jays were captured, including one from Orange county.

Handling protocol. Jays captured in the morning were immediately weighed, measured, and outfitted with a transmitter, then observed in a large flight cage for several hours to allow the bird to become accustomed to the backpack harness. Jays captured in the afternoon were held overnight and processed the following morning. Jays were

transported to their release sites in cages covered with heavy material to prevent the jays from seeing the passing landscape and thereby potentially developing a homing direction. All jays were released in the late afternoon.

Radio-transmitters were mounted with a technique already in use by another researcher (Keith Tarvin) on Blue Jays at Archbold Biological Station. A 2-g transmitter (manufactured by Wildlife Materials of Carbondale, IL) was mounted on the back of each jay and secured with elastic cord. The transmitters had small tubes on the front and back that the cord was run through to create a loose, independent loop of equal size around each wing. A small loop of cord was run between the wing loops and across the belly to make the harness snug. The cord was kept loose enough to avoid cutting into the skin or restrict movement or breathing, but tight enough to eliminate slack cord that feet or branches might catch on. Newly outfitted jays were observed in an outdoor aviary for at least half a day, and sometimes overnight. When initially rigged, jays were preoccupied with trying to remove the outfit, suggesting that initially they might be especially vulnerable to predators. Properly fitting harnesses were ignored after a few hours and more normal behave resumed – including taking peanuts and drinking water. My failure to tie the knots on the harness tightly occasionally allowed jays to untie and remove the transmitter, but only while in the aviary. I used forceps to cinch knots tightly to reduce their size; knots were placed away from areas where they might rub against pressure points. The elastic cord, obtainable from many fabric stores, degrades and falls apart within a year or so; one jay that returned to Archbold wore her transmitter for a year before it finally fell off. Her antennae also broke off after several months (reinforcing each antennae base with epoxy might have been beneficial). Since most electronics fail

during an initial burn-in period, I activated each transmitter for a 24 hour test period prior to use. Nevertheless, several transmitters appear to have failed after only 1-2 days in the field.

Release sites. Radio-tagged jays were released at three different sites: a ranch setting, a citrus grove, and a suburban area. The ranch setting was the MacArthur Agroecology Research Center. The citrus grove setting was adjacent to and west of U.S. 27, north of S.R. 70, and south of the city of Lake Placid, Highlands county, Florida. The suburban setting was the center of the city of Lake Placid.

Sampling protocol. I followed jays continuously on the first day of release until they went to roost. Thereafter jays were visited on a schedule dictated by their activities. Jays were visited at least three times daily regardless of activity: in the early morning, in the early afternoon, and near dusk. During periods of active movement, jays were followed intensively until large movements ceased. Visual contact could be maintained for many long movements, since jays typically flew above visual obstructions such as shrubbery. Locations of moving jays were plotted in the field on 1:24000 aerial photos, using landmarks visible in the field and on the photos. When visual contact was lost, triangulation was ineffective for plotting locations, since multiple bearings could not be taken before a jay had moved large distances. Visual contact was often reestablished by moving to a position ahead of the jay's last known trajectory and awaiting its reappearance. One jay moved onto large private landholdings that could not be accessed by land. Airplane overflights were used once or twice daily (N=6 days) to establish its movement at a coarse scale.

Transmitter effects. Subsequent to my conducting the displacement experiments, Reed Bowman (pers. comm.) compared the behavior of jays outfitted with 2 types of transmitters: backpack harnesses like those used in this study and leg mounted transmitters. He observed substantial behavioral differences between jays with backpacks and jays with leg-mounted transmitters. Jays with backpacks showed periods of immobility lasting hours or even days punctuated by periods of more normal movement. This behavior was quite different from birds with leg mounts, which acted normally compared to several untagged jays that served as controls. None of Bowman's jays were artificially displaced from their natal territory. I also observed long periods of inactivity (Fig. 4-1), but because my jays were displaced into completely unfamiliar settings, I could not evaluate whether their inactivity resulted from the transmitter or was a behavioral response to being displaced. I suspect the backpack outfit did reduce the activity of displaced jays, but I have no reason to think that the backpack impeded their movements once the jays became active. Therefore, to estimate the mobility of jays I excluded days with no jay movement.

Constraint Analysis

Dispersal events recorded (or known to be absent) in the vicinity of Archbold Biological Station were used to place constraints on several long distance dispersal parameters. A small but stable population of jays occurs some 20 miles (33.32 km) due west of Archbold Biological Station on the Bright Hour Ranch, in DeSoto county. The intervening habitat consists of palmetto flatwoods, small wetlands and seeps, citrus groves, and improved and unimproved pasture. Several surveys of this locality during the 1980's and early 1990's (by Fitzpatrick et al.) have revealed no dispersals from

Archbold Biological Station. Furthermore, the vocalizations of these jays are noticeably different from Archbold Biological Station jays, suggesting that this population is genuinely isolated from the Lake Wales Ridge population. Therefore, a reasonable constraint to place on the dispersal module is that few or no floaters from Archbold Biological Station (or contiguous Lake Wales Ridge populations) can disperse successfully as far as the Bright Hour Ranch. A second constraint in the opposite direction can be placed on the model. A small number of dispersals have been documented that are considerably longer than the distance separating Archbold Biological Station from Bright Hour Ranch. These include jays color-banded at Archbold Biological Station and Avon Park Air Force Range, several of which dispersed between 35 and 50 km. The dispersal module should produce at least a few colonizations by Archbold floaters to distant patches; such colonizations will show up in the dispersal curve generated by the model.

The objective of the constraint analysis was to identify parameter settings that prohibit dispersals from Lake Wales Ridge populations (around Archbold Biological Station) to Bright Hour Ranch, while allowing longer dispersals to areas where color-banded jays are known to have become breeders. Simulations were run that included the territories in and around Archbold Biological Station and at the Bright Hour Ranch. The number of dispersers that successfully located the Bright Hour Ranch were tabulated for each run. Several floater parameters were varied, including the detection radius, the maximum daily distance traveled, the daily mortality rate, and the rate of floater formation ($P_{floater}$; varied by sex and age). Two types of daily mortality rates were used: a Kaplan-Meier distribution, and a fixed mortality rate.

Model Validation

Model validation was performed by comparing model output with dispersal and stage-age data from long-term research at Archbold Biological Station. Kolmogorov-Smirnov tests were used to measure the goodness of fit between the simulated frequency data and those of the Woolfenden and Fitzpatrick study. The dispersal field data for male jays that dispersed by territory budding were lumped with jays that dispersed one territory. This was necessary because the model does not simulate budding. I also provide a qualitative assessment of other aspects of the model.

Results

Radiotelemetry Displacement Experiment

Of 10 female helpers released in non-scrub habitat, 4 were apparently depredated (3 probably by accipters, 1 probably by domestic cat), 1 became ill after 2 days and was recaptured, 3 successfully returned to their Archbold Biological Station home territories, and 2 disappeared for unknown reasons. Premature transmitter failure is suspected for the latter 2 disappearances (after 2 and 6 days). Premature transmitter failure was known to occur in 2 of 3 jays that returned to Archbold Biological Station (failures after 2 and 13 days). The 4 apparently depredated jays survived 1, 3, 4, and 22 days. Jays generally made large movements over a period of one or two days, followed by one or more days of relative inactivity. During periods of large movements (defined as greater than 0.33 km), jays moved an average of 5.2 km/day (range = 0.42 to 19.9 km).

Of three jays released at a citrus site, one was depredated by an accipter on day 2 of its release after moving 1.25 km, and two jays used citrus and a scrubby railroad corridor to return to Archbold Biological Station. All jays released at the citrus site behaved secretively, mostly made small movements, and stayed in citrus rather than crossing US-27 (a divided 4-lane highway) to nearby sandhill habitat. They showed no tendency to use the edges of groves, and readily flew through and roosted in interior portions of groves. Five jays crossed expanses of citrus of 1.66 km or more.

Of three jays released in a ranch setting (improved pasture with cabbage palm /oak hammocks), one was apparently depredated by an accipiter, and two disappeared after 2 and 6 days, possibly due to transmitter failure. All ranch jays made large movements from hammock to hammock, never were observed crossing expanses of open pasture greater than 200 meters, and never ventured far into the interior of any large hammocks. While moving or resting around large hammocks, they were always at or near the hammock edges. One ranch-site jay found and settled in a nearby citrus grove for 2 days before disappearing. The other 2 jays roosted at edges of oak hammocks, and seemed preferentially to select smaller, isolated oak hammocks (data were insufficient for statistical analysis).

One jay released at the ranch (R-MF) engaged in highly unexpected roosting behavior. On the morning following her release, the transmitter signal was originating from below ground within decaying palm frond sheaths at the base of a small, dead cabbage palm. After waiting until 08:15 seeing no sign of activity, I fully expected that the jay had been captured and eaten by a snake, and began excavating the palm and removing ground debris to retrieve the transmitter. Suddenly, R-MF flew out into my

face from a point at least 30 cm underground. She appeared to behave normally thereafter, and roosted in cabbage palms high off the ground on at least one other occasion.

All observed movements of ranch jays were relatively short, from tree to tree. No continuous, sustained flights greater than about 500 m were observed. Jays making movements larger than 500 m tended to move in a hop-scotch manner from treetop to treetop, stopping frequently along the way for short periods (often less than 1 minute) to survey their surroundings. If they flew to a large tree, either they would fly to the top of the tree or, if landing lower on the tree, would usually work their way up to the tree top and look around before moving on.

Of four jays released in downtown Lake Placid, one successfully returned to Archbold Biological Station via a large tract of scrub and pine (her transmitter failed after day 1 and she was discovered back home months later during a census), 1 was apparently injured by an accipiter and died one day later, another was apparently killed by a cat on day 4, and a fourth became noticeably ill (was seen regurgitating food) and was recaptured on day 2. All downtown jays tended to move in a hopscotch manner from treetop to treetop. Two downtown-site jays found jays within 2 days about 4.15 km to the southwest in the heavily developed Lake Placid suburb after crossing about 2.5 km of downtown Lake Placid and 166 km of citrus.

Table 4-4 summarizes the movement data for each radiotagged jay. Figure 4-1 shows the daily movement and the number of days each jay was alive. Several jays show day-long periods of inactivity followed by large movements. Three jays were right-

censored in the figure because they successfully returned to their home territory. The remaining jays either perished or were lost due to transmitter failure.

A Kaplan-Meier survival curve (Fig. 4-2) shows the daily probability of survival for the pooled sample of jays. Three survival curves were generated by making different assumptions about unknown disappearances. The upper curve assumes that all unknown disappearances were caused by transmitter failure, the bottom all due to mortality, and the middle curve makes an "educated-guess" about each disappearance based on circumstantial evidence. The 3 jays that successfully returned to their home territory were right-censored. All three curves show an early rapid decrease in survivorship caused by known mortality of several jays shortly after release. The constant daily survivorship out to day 21 reflects a single jay released at the ranch which was depredated at day 22.

Floater Parameter Estimation

Floater mobility was parameterized by fitting a function generated by the curve fitting procedure of SPSS (ver. 7.5) to the distribution of daily distances (Fig. 4-3) moved obtained from radiotelemetry field data (excluding days with no movement – see explanation above). An inverse function of the form $x = b1/(y - b0)$ produced a good fit with the observed data ($r^2 = 0.851$; $F = 91.43$; d.f. = 16; $p = 0.000$). Values for the two coefficients were: $b0 = -0.48$; $b1 = 5.57$.

Daily survival of floaters within scrub was assumed to be only slightly less than survival of non-dispersing stages, as measured at Archbold Biological Station. The default daily survival value was set at 0.9988, which was computed from the estimated annual survival rate of 2nd year female helpers ($0.66^{\cdot 365}$). Daily survival of floaters

outside scrub was parameterized with the "best-guess" Kaplan-Meier curve (Fig. 4-2) generated from the radiotelemetry field data.

Other floater parameter values were estimated indirectly, and are listed in table 4-5. The selection of these values is described in the Methods section.

Constraint Analysis

The constraint analysis provided a valuable upper bound for several of the floater dispersal parameters (table 4-5). An unrealistically high number of dispersals from the Lake Wales Ridge to the Bright Hour Ranch occured for parameter settings that are not substantially higher than the default settings (table 4-5).

Calibration and Validation

Comparisons between model output and dispersal data obtained from long term observations of marked jays (unpublished data provided by J.W. Fitzpatrick and G.E. Woolfenden) are shown for male and female dispersal in Figs. 4-4 and 4-5. The general shapes of the dispersal curves produced by the model closely resembled the field data. Model output did not differ significantly for females and was marginally different for males compared to the field data (Kolmogorov-Smirnov: male $Z = 1.373$, $p = 0.046$; female $Z= 0.784$, $p = 0. 570$). Comparisons between model and field data for age-stage structure of helpers and breeders are shown in Figs. 4-6 and 4-7 (obtained from tables 9.8 and 9.9 in Woolfenden and Fitzpatrick 1984). Model and field data comparisons are not significantly different for helpers or breeders (Kolmogorov-Smirnov: breeder $Z = 0.447$, $p = 0.988$; helpers $Z= 0.267$, $p = 1.00$).

Discussion

Each of the behavioral rules (table 4-3) implemented in the software to generate dispersal and stage-age curves similar to the Archbold field data has clear biological meaning and is readily matched to features of known jay biology. Early versions of the model, incorporating simpler rules, produced dispersal curves quite different from the Archbold data. Interestingly, some of these curves were more similar to dispersal curves for non-cooperative species. The final set of rules seems to capture key elements of dispersal behavior that may partly account for differences between cooperative and non-cooperative species. For example, after reviewing bird studies with adequate dispersal data, Zack (1990) found that cooperative species dispersal distances were strongly skewed towards the natal territory compared to non-cooperative breeding species. Dispersal curves generated by early versions of my model resembled non-cooperative species in that the mode was several territories away from the natal territory. This pattern arose when the probability of settling on a vacancy was nearly the same for any territory within an individual's assessment sphere. To produce the strongly right-skewed pattern of a cooperative breeder, rules must be added to increase the probability of acquiring nearby vacancies rather than those that are more distant within the assessment sphere. Algorithmically, I simulated this behavior by keeping a distance-sorted list of nearby territories within each disperser's assessment sphere. When a breeder death creates a vacancy, the helper closest to that territory was given "first choice" at the opening (ties were broken by random draw). This dominance hierarchy is further modified to account for age by processing older helpers before younger. These rules are summarized in table 4 – 3.

The biological consequence of these philopatric dispersal rules is that they increase the probability that dispersers engaging in delay-and-foray behavior will acquire a nearby vacancy. A fascinating controversy relating to this feature exists in the literature on the evolution of delayed dispersal. Experts on the Florida Scrub-Jay attribute the origins of this behavior to "ecological constraints": under normal conditions high quality jay habitat is fully occupied ("saturated"). Survival and fecundity of dispersers outside of high quality habitat is so low that it is better to remain at the natal territory and maximize opportunities for acquiring nearby vacancies in the future. While acting as resident helpers, jays can engage in behavior that increases their likelihood of acquiring a territory. Such behavior includes engaging in frequent short forays to investigate potential vacancies due to a breeder death or illness, enlisting the help of parents and siblings to "bud" a territory, establishing dominance over nearby helpers (potential competitors), developing "furtive" relationships with neighboring opposite sex breeders, and learning territory boundaries, refugia from predators, and roost sites. Besides these "direct" benefits to staying home, certain "indirect" benefits accrue by helping relatives (Woolfenden and Fitzpatrick 1984). Zack (1990), Stacey and Ligon (1991), Brown (1989) and others present these factors as "benefits of philopatry", and argue that they are more important than "ecological constraints." Krebs and Davies (1998, p. 304) suggest that the two views are "not so much alternative hypotheses as different sides of the same equation". They suggest that the pay-offs depend on the quality of breeding vacancies available and how much competition exists.

Carmen (1989) showed that Western Scrub-Jays do not engage in delay-and-foray dispersal behavior. In some cooperative breeders dispersers show considerable

behavioral flexibility. For example, in the Seychelles warbler (*Acrocephalus sechellensis*), dispersers from high quality territories delay dispersal when high quality territories are unavailable, while dispersers from low quality territories, where survival is low, do not delay dispersal but instead settle for a low quality territory (Komdeur 1992). Florida Scrub-Jays do exhibit some flexibility in dispersal, as suggested by the behavior of suburban jays. For example, Bowman (1994), Thaxton and Hingten (1995), and Breininger (1999) have documented traits in suburban jays that have much in common with the "floating" behavior of the Western species, including reduced delays in dispersal and much greater dispersal distances. Within good habitat "floating" behavior in Florida Scrub-Jays is likely to be rare, but fire suppression may lower habitat quality sufficiently to encourage floating , and excessive numbers of helpers at a territory might encourage subordinates to disperse early (so-called "saturation dispersal"). The possibility that Florida Scrub-Jays may switch between these two dispersal strategies needs further investigation.

The telemetry displacement study provided a number of useful findings that were incorporated into the floater module. Jays clearly avoided open habitats lacking tree or shrub cover, such as water bodies and pasture. In contrast, they moved freely through a variety of landscapes with at least some tree or shrub cover, including citrus groves, sandhill, pasture with small, scattered oak hammocks, and suburbs with trees. This information was incorporated into the model by assigning different attractiveness values to various landcover classes based on the amount cover each class is likely to provide. Table 4-3 shows the original landcover classes encoded in the Florida Game and

Freshwater Fish Commission's statewide classification, and each class's respective attractiveness value as assigned by me following the telemetry study.

The animation graphics displayed during a simulation run allows the movement of long distance dispersers to be visually checked. Dispersers behaved as expected, completely avoiding landcover types with highly repulsive values, moving in an essentially straight line in habitat with neutral attractiveness, and preferentially turning towards habitat with high attractiveness values. Simulated floaters could be observed moving long distances, and the dispersal curves generated by the program showed that they occasionally settled after moving long distances.

Quantitative comparison of movement patterns generated by the model with those recorded for radiotagged jays was not feasible because the sample size, resolution of data recorded, and movements of several jays all were too small for meaningful statistical tests. Simple circular statistics could be used with a better data set to test jay movements for directional bias (Batschelet 1981; Zar 1996). Turchin (1998) outlines several more sophisticated analyses, but besides requiring better data sets, Turchin's analyses are designed to test for correlated random walk, which is more typical of insects than the landscape-directed movements of vertebrates. Statistical tests appropriate for this model probably do not exist, and would likely involve boot-strap tests based on simulations developed for specific landscape settings.

Although Florida Scrub-Jays are fairly weak fliers (Woolfenden and Fitzpatrick 1996), jays that were experimentally displaced were capable of moving fairly long distances, up to a maximum of 20 km per day, with an average daily movement of about 2.67 km. This information was used to parameterize the daily movement parameter in the

floater algorithm, and the constraint analysis suggested that actual movements should not be much larger than the measured distribution.

The constraint analysis showed that simulated jays originating from Archbold or nearby patches rarely colonized the Bright Hour Ranch for certain parameter settings, even though the dispersal curve showed that some Archbold dispersers did succeed in settling much greater distances within the Lake Wales Ridge than the distance to Bright Hour. This bias in dispersal success is largely due to the floater mortality rates set in the model for different habitat types; jays that moved the longest distances were those that managed to stay in scrub habitat the longest.

The displacement experiment suggested that jays suffered much higher mortality rates while moving through non-scrub landscapes than they would likely experience in scrub habitat. Predators took several jays, and it is possible that several other jays that vanished inexplicably were also predated. These losses suggest that dispersal outside scrub habitat is a costly activity for Florida Scrub-Jays, which is consistent with other findings and a suite of behavioral traits described earlier, including the sentinel system, delayed dispersal, and unusually short dispersal distances. The Kaplan-Meier curve developed from the radiotelemetry data provided strong evidence for the vulnerability of jays to predation in unfamiliar, non-scrub habitat. The Kaplan-Meier curve also provided a useful means of parameterizing the daily survival of floaters (fig. 4-2), and demonstrated graphically the potentially high cost of long distance dispersal through unfamiliar terrain. The mortality rates measured for displaced jays are extremely high, and likely are higher than would be experienced by naturally dispersing, untagged jays due to negative effects of the backpack harness and radio transmitter. Nevertheless, the

constraint analysis suggested that floater mortality rates outside of scrub must be high, otherwise unrealistically high colonization rates to Bright Hour Ranch occurred. The constraint analysis also indicated that a fixed daily survival rate of 0.75 or higher for floaters outside of scrub produced excessive colonizations, assuming the default movement function. In combination, the field derived Kaplan-Meier curve (Fig. 4-2) and movement function (Fig. 4-3) produced satisfactory results in the constraint analysis.

The statistical comparison of model output with long-term field data (fig. 4-3 to 4-6) gave mixed results, showing no significant differences for the stage-age data, but marginal differences for the dispersal data. Even though the dispersal curves bordered on being statistically different, the similarity of the simulated and field data is obvious, showing the same mode and the appropriate differences between male and female dispersers. A consistent bias is apparent in the simulated data, which shows too few dispersers at the mode and too many dispersers just after the mode for both sexes. Incorporating "budding" into the model might correct these biases.

Although statistical attempts to validate the model were equivocal, other means of validation are available. In a comprehensive review of different ways of validating ecological models Rykiel (1996) argues that qualitative assessments such as "face validation" (the approval of an experienced field person) often are adequate. Lima and Zolner (1996) suggest that qualitative assessments may have to suffice for evaluating models of complex interactions between animal behavior and landscape ecology, at least until the hard-to-acquire data sets become available and techniques such as those proposed by Turchin (1998) are developed. Qualitatively, the dispersal module compares favorably with other models in terms of complexity. A literature search revealed only one

other model (Letcher et al. 1998) that simulates both philopatric and floater dispersal. No models were found that generated dispersal and stage-age distributions to compare with field data. The level of detail and biological realism in this model are high due to the availability of long term research data and crude telemetry data. The constraint analysis proved valuable in placing bounds on acceptable parameter settings. Nonetheless, numerous simplifying assumptions were made, as is true of any model. A full discussion of the model's assumptions is given in chapter 5, which describes the complete model. The evaluation of the dispersal module presented in this chapter exemplifies a useful technique of separately validating individual model components (Thomas et al. 1990). Nonetheless, it is important to investigate the sensitivity of the overall model to potential errors in the dispersal module and other model components. Such comparisons may reveal that the model is crucially or inconsequentially affected by the dispersal module.

Table 4–1. Landcover types from statewide habitat map (Kautz et al. 1993) used in simulations and associated floater attractiveness values.

Landcover Type	Attractiveness Value[a]
Coastal Strand	3
Dry Prairies	1
Pinelands	2
Sand Pine Scrub	2
Sandhill	2
Xeric Oak Scrub	4
Mixed Hardwood Pine Forest	1
Hardwood Hammocks and Forests	1
Tropical Hardwood Hammock	1
Coastal Salt Marshes	1
Freshwater Marsh and Wet Prairie	2
Cypress Swamp	1
Hardwood Swamp	1
Bottomland Hardwoods	1
Bay Swamp	1
Shrub Swamp	2
Mangrove Swamp	2
Aquatic	0
Grassland	1
Shrub and Brushland	2
Exotic Plant Communities	2
Barren	0

a Attractiveness values range from 0 to 4 (0 = repulsive; 1 = unattractive; 2 = neutral; 3 = attractive; 4 = highly attractive).

Table 4–2. Demographic parameters used to estimate the proportion of disappearing helpers that become floaters.

Age Class	D_{total} [a]	D_{eq} [b]	$E_{nonlocal}$ [c]	$E_{nonlocal}/D_{total}$ [d]	$P_{floater}$ [e]
Male Yearling	0.225	0.22	0.005	0.022	0.022 – 0.75 (0.25)
Female Yearling	0.42	0.35	0.07	0.167	0.167 – 0.75 (0.75)
Male 2nd Year Helper	0.25	0.15	0.10	0.40	0.40 – 0.75 (0.50)
Female 2nd Year Helper	0.375	0.26	0.115	0.307	0.307 – 0.75 (0.75)

a D_{total} is the observed proportion of total disappearances (from Woolfenden and Fitzpatrick 1984; Table 9.5; p. 275).

b D_{eq} is the equilibrium mortality rate (from Woolfenden and Fitzpatrick 1984; Table 9.5; p. 275).

c $E_{nonlocal}$ is the proportion of total disappearances due to dispersers becoming breeders elsewhere as unobserved emigrants (from Woolfenden and Fitzpatrick 1984; Appendix M) calculated as D_{total} - D_{eq}.

d $E_{nonlocal}/D_{total}$ is the proportion of D_{total} estimated to become breeders elsewhere as emigrants. This value sets a lower limit for $P_{floater}$.

e $P_{floater}$ is the proportion of D_{total} becoming floaters. A plausible range of values is listed first, followed by a "best guess" in parentheses.

Table 4–3. Summary of philopatric dispersal rules showing sex differences and rules used to implement the algorithm.

Male	Female	Algorithmic implementation
Smaller "assessment sphere"	Larger "assessment sphere"	Only move to vacancies within the specified assessment sphere.
Natal Inheritance	No natal inheritance	If both breeders die, resident male helper has priority over nonresident male helpers.
Extreme competitive advantage near home	Nominal competitive advantage near home	Sort territories within assessment sphere by distance. Allow each female to select nearest vacancy within assessment sphere. For males, divide sphere into 3 nested subspheres. Process each subsphere separately, innermost to outermost. Allow each male to select nearest vacancy within each subsphere.
Prefer unpaired breeders over vacant territories	Prefer unpaired breeders over vacant territories	Complete search for unpaired breeders for all dispersers before searching for vacant territories.
Older helpers dominate yearling helpers	Older helpers dominate yearling helpers	During search for unpaired breeders or vacant territories, process all older helpers before yearling helpers.

Table 4–4. Summary of jay movement data obtained from displacement experiment (distances in km).

Jay color band id	Territory of origin [a]	Release site [c]	Max. daily movement [d]	Active mean daily movement [e]	Inactive mean daily movement [f]	Cumulative distance traveled	Start-end dist [g]	Days moving [h, i]	Days alive [j, k]
G-MR	MIDR	1	1.25	1.25	1.25	1.25	1.0	1	1
GZ-O	EERR	1	8.33	2.97	1.22	12.2	6.67	4 [6]	[10] {ABS}
YB-GM	Disney [b]	2	15 - 20	5.33 - 5.83	2.33 - 2.67	53.3 – 58.3	3.33	10	22
R-MO	BYRD	2	(4.17)	(4.17)	(2.17)	(4.17)	(4.17)	(1)	(1)
R-MF	TP68	2	(4.17)	(2.0)	(1.03)	(6.17)	(1.66)	(3)	(6)
R-MA	CWHP	1	(1.67)	(0.77)	(0.30)	(3.83)	19.2	(13)	{ABS}
LZ-A	DEAD	3	4.17	4.17	1.38	4.17	4.17	1	3
Y-MW	MARE	3	2.58	2.42	1.22	4.83	1.00	2	4
Y-CR	DRUM	3	0.42	0.38	0.38	0.75	0.75	2	2
Z-YY	TRVN	3	(4.67)	(2.38)	(2.38)	(21.7)	16.6	(1)	{ABS}
Mean			(4.67 - 5.17)	(2.60 - 2.63)	(1.37 - 1.40)	(11.2 - 11.7)	5.83	3.3	3.9

a Territory of origin from the south ("experimental") tract of Archbold Biological Station.
b Jay obtained in mitigation deal from Disney property in Orange Co., Florida.
c Release sites (Highlands county, Florida): 1 = Large citrus grove with nearby sandhill on W. side of Grassy Lake; 2 = MacArthur Agroecology Research Center - improved pasture and numerous cabbage palm/oak hammocks; 3 = Downtown Lake Placid.
d Numbers in parentheses indicate distances or days measured for birds lost for unknown reasons.
e Days when birds were not moving were excluded in distance calculations.
f All days were included in distance calculation, including days with no movement.
g Straight line distance between release site and last known location.
h Number of days when bird moved more than 0.33 km.
i Numbers in brackets include days when jays were in scrub habitat.
j Number of days jays were known to be alive. See *d* and *i* for explanation of numbers in parentheses or brackets.
k {ABS} indicates jay successfully returned to its territory of origin at Archbold Biological Station.

Table 4–5. Summary of constraint analysis for 9 simulation scenarios (50 years x 30 repetitions) showing number of colonizations from Lake Wales Ridge to Bright Hour Ranch, DeSoto county, Florida.

Search Radius[a]	Survival[b]	Max. Distance[c]	$P_{floater}$[d]	Colonizations[e]
10	Kapl	400	0.25/0.75	2
10	Kapl	500	0.15/0.55	4
10	Kapl	500	0.25/0.75	3
10	Kapl	600	0.25/0.75	13
20	Kapl	500	0.25/0.75	7
10	0.50	500	0.25/0.75	2
10	0.70	500	0.25/0.75	22
10	0.90	500	0.25/0.75	65
10	1.00	500	0.25/0.75	225

a Distance in 30 m pixels dispersing jay “sees”.

b Daily survival rate: Kapl. = Kaplan-Meier data (fig. 4-2); Numbers = daily survival

c Maximum daily distance traveled by floater (units for inverse function – see text).

d Probability of disappearing helpers becoming floater (male/female).

e Number of dispersers finding Bright Hour Ranch from Lake Wales Ridge

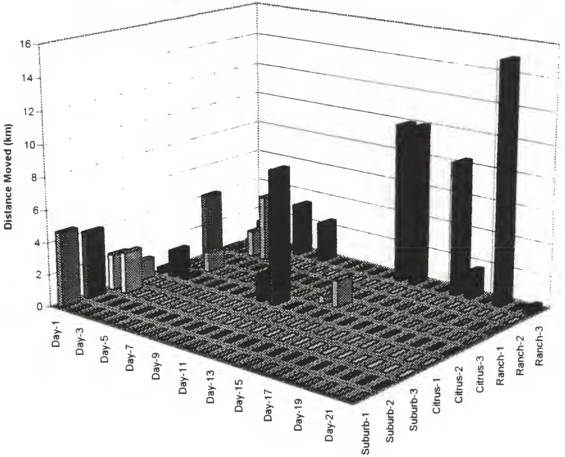


Fig. 4-1. Daily distances moved and number of days movements were tracked for 10 jays released at 3 sites in Highlands county, Florida.

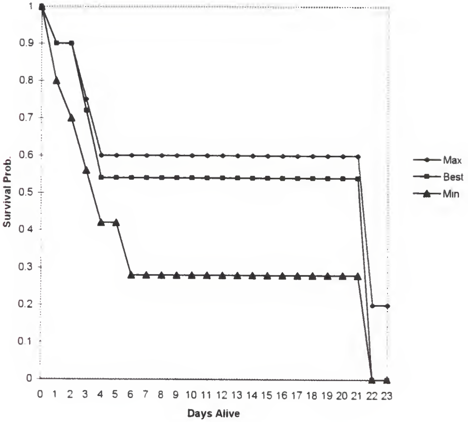


Fig. 4-2. Kaplan-meier survival curves of daily survival rates for 10 jays released at 3 sites in Highlands county, Florida. Upper curve: maximum possible survival; middle curve: "best guess" survival; lower curve: minimum possible survival.

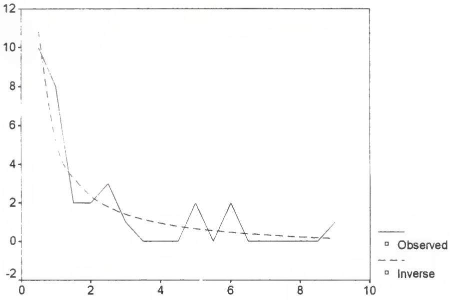


Fig. 4-3. Distribution of daily distances moved by released jays (solid line), and inverse function fitted to observed movements (dashed line).

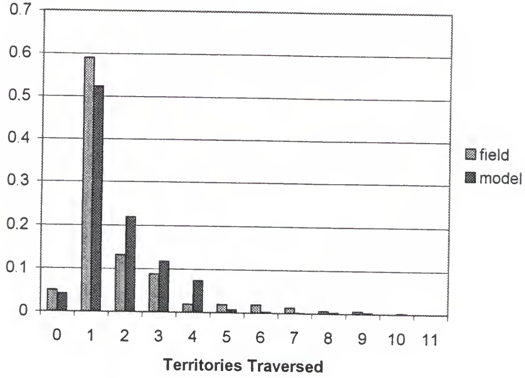


Fig. 4-4. Comparison of dispersal data from Archbold Biological Station and simulated dispersal distances for male jays.

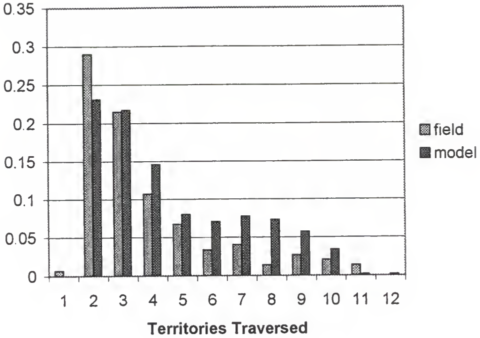


Fig. 4-5. Comparison of dispersal data from Archbold Biological Station and simulated dispersal distances for female jays.

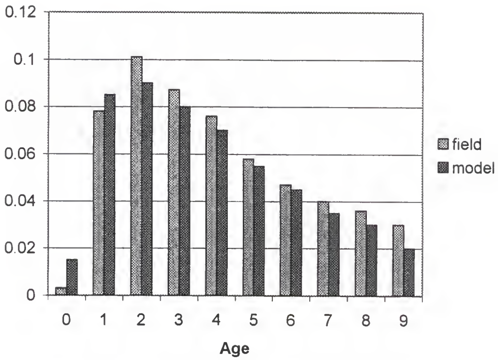


Fig. 4-6. Comparison of stage-age data from Archbold Biological Station and simulated stage-age data for breeders.

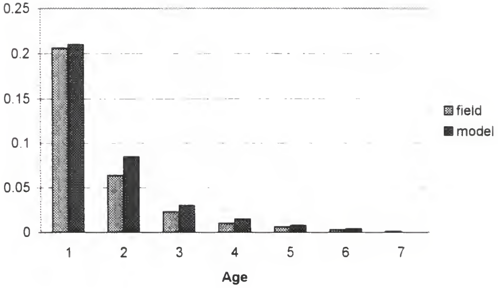


Fig. 4-7. Comparison of stage-age data from Archbold Biological Station and simulated stage-age data for helpers.

CHAPTER 5
METAPOPULATION VIABILITY ANALYSIS OF THE FLORIDA SCRUB-JAY

Introduction and Objectives

The Florida Scrub-Jay is a Federally threatened bird species that occurs only in Florida. Formerly found in 39 of 40 counties of peninsular Florida, by 1981 the Florida Scrub-Jay was known to be extirpated from 7 counties (Broward, Dade, Duval, Gilchrist, Hendry, Pinellas, and St. Johns; Cox 1987). A 1992-1993 statewide mapping project (SMP) added Alachua and Clay to the list of extirpations, and estimated that less than 10 breeding pairs remained in 6 other counties (Flagler, Hardee, Hernando, Levy, Orange, and Putnam; Fitzpatrick et al. 1994). In nearly all other counties jay populations have declined drastically. Since 1993, a severe decline to near extinction was documented on the barrier island south of Patrick Air Force Base in Brevard county (Breininger 1999), and a huge decline exceeding 50% was documented on mainland S. Brevard county during the same period (Breininger 1998). Undoubtedly, similar drastic declines are occurring throughout the state. Humans are directly responsible for this dramatic population reduction, primarily through suppression of natural fires which are necessary to maintain high rates of reproduction and survival in scrub-jay populations, and through outright destruction or degradation of jay habitat due to roads, housing developments, and agriculture (e.g. citrus groves).

Although these negative population trends are severe, opportunities still exist to acquire, restore, and manage occupied habitat in various portions of the scrub-jay's rapidly dwindling range. The 1992-1993 SMP, analyzed in chapter 2, showed that the Florida Scrub-Jay has a highly variable spatial distribution around the state, resulting in complex metapopulation structure associated with the wide range of local population sizes and varying degrees of isolation. This variability in spatial structure undoubtedly has strong effects on the ability of jays to persist within different landscapes. Faced with this complexity, the question arises: which populations of scrub-jays are adequately protected, and what additional land acquisitions are needed in areas where jays are not adequately protected?

The answer to this question will depend not only on the influence of the spatial distribution of jays and their habitat, but also the demographic success of the jays within a given landscape context. Empirical research and population modeling has shown that the demographic performance of jays varies considerably due to habitat features such as the degree of vegetative overgrowth (Fitzpatrick and Woolfenden 1986; Woolfenden and Fitzpatrick 1991; Breininger et al. 1995, 1996) and the extent of human disturbances such as road mortality (Mumme et al. in press). Indeed, fire suppression alone has been shown to guarantee extinction, even in large populations (Root 1998; Breininger et al., in press). Thus, habitat acquisition alone will not ensure survival of jays; proper habitat management is also critically important. Ascertaining which jay populations have the greatest need for land acquisition is, therefore, complicated by the fact that many of the currently protected areas have not been properly managed, and could support more jays. Research and management experience has shown that local declines in scrub-jay

populations can be reversed in areas that are restored to optimal habitat conditions and properly managed (J. Thaxton, pers. comm.; D. Breininger, pers. comm.). The critical importance of optimal habitat to jays is becoming widely recognized, and initiatives to manage protected areas for scrub-jays are rapidly gaining momentum. If these protected areas were restored and jay populations increased to higher densities, how viable would jay populations be with and without further land acquisition? Given the complex distribution of scrub-jays, which areas are most in need of further acquisition, and which habitat patches should be acquired?

These are the primary questions addressed in this chapter. The classification technique developed and applied for metapopulations around the state (chapter 2), while useful for describing the spatial structure, cannot provide viability estimates for the various metapopulations. This chapter describes the application of a spatially explicit, individual based population model (SEIBPM) to estimate the viability of Florida Scrub-Jay metapopulations. SEIBPMs take into account site specific details of habitat distribution and habitat quality, and provide a standardized, scientific framework for answering questions relating to the viability of organisms in different reserve configurations. SEIBPMs are a very new form of computer technology and are not without their problems (Beissinger et al. 1998). Nevertheless, these models can produce quantitative information that is obtainable in no other way, and when used properly can provide invaluable information that supplements and informs more conventional approaches to land acquisition and land management.

Objectives: The primary objectives of this chapter are:

- Compare the relative vulnerability of different jay metapopulations around the state. Use measures of vulnerability, such as quasi-extinction risk and percent population decline, to rank the vulnerability of jays in different parts of their range.
- Compare the relative vulnerability of different configurations of jay populations within the same metapopulation. Model different spatial configurations of jay metapopulations, ranging from a "no additional acquisition" configuration to a "maximum acquisition" option.
- Identify unprotected areas that would significantly increase the expected persistence of each metapopulation if they were acquired, restored, and properly managed.

Methods

Simulation Model Description

All simulations were performed with a spatially explicit, individual-based population model written by B. Stith specifically for the Florida Scrub-Jay. The model was developed using Microsoft Visual C++ (ver. 5.0) for use on Intel-compatible personal computers running Microsoft operating systems (Windows 95, 98, and NT 4.0). Simulations of jay population dynamics take place on realistic landscapes provided by geographic information system (GIS) files. The model incorporates general aspects common to many population models, including demographic and environmental stochasticity, as well as a host of details specific to scrub-jay biology.

Because of striking differences in the biology of male and female jays, both sexes are modeled. Except when dispersing, simulated jays reside within discrete territories. Individual jays of both sexes progress through 5 life stages (juvenile, 1-year helper, older helper, novice breeder, and experienced breeder). Breeder experience and presence of helpers affects breeder success. Helpers monitor neighboring territories and vie for breeder openings; the outcome of such competition is determined by simple dominance rules. Helpers may leave on long distance dispersals, during which time mortality and movement varies depending on the type of landcover being traversed. During the simulation, graphs of dispersal distances, stage-age structure, population trajectory, and quasi-extinction probabilities are displayed, and text descriptions of various events occurring during the simulation can be viewed and saved to an output file.

Life Stages

Each territory maintains a list of all individuals of both sexes in the following 5 stages:

- Juvenile
- 1-Year Helper
- Experienced Helper
- Novice Breeder
- Experienced Breeder

Helpers can transition into a sixth stage by departing from their natal territory and becoming a long-distance disperser ("floater").

Starting Population Stage Structure

At the start of each repetition of each simulation run, all territories are initialized with a pair of inexperienced breeders (both 2 years old) and one inexperienced helper (1 year old; randomly selected sex). The location of each territory is obtained from an ASCII file provided to the model (see GIS section below).

Annual Life Cycle

The scrub-jay annual life cycle is simulated by a series of events scheduled in an event queue; each event is completed for the entire metapopulation before the next event begins. The following is a summary of the major events in the annual cycle, which begins with reproduction.

Reproduction. Each territory produces a poisson distribution of juveniles (see Burgman et al. 1993) with 3 different means (see Table 5-1) for: 1) at least one experienced breeder with at least one helper, 2) at least one experienced breeder but no helpers, or 3) both novice breeders. The fecundity parameter values are set to the number of one-year old offspring produced, rather than fledglings produced. From a software efficiency standpoint, this greatly reduces the number of jays that must be created and then destroyed in the mortality step that immediately follows (i.e. the model does not subject juveniles to mortality during their first year – the fecundity rate accounts for this mortality). Demographic stochasticity of fecundity is implemented by randomly selecting the sex of offspring. Environmental stochasticity of fecundity is not implemented, but would be expected to have a negative effect on population persistence.

Field studies have shown that in the Florida Scrub-Jay, environmental stochasticity of fecundity and mortality are positively correlated (Woolfenden and Fitzpatrick 1984).

Annual mortality. Breeder and helper annual mortality rates are based on the current territory configuration (see Table 5-1). All breeder vacancies available to dispersers are created in this step. Helpers do not actually die in this step, but are considered to have "disappeared." The "floater frequency" parameter later determines whether they die or become floaters (see dispersal section below). Juveniles are not subjected to mortality in this step since their annual mortality is already reflected in the fecundity rate. Epidemics occur with an annual probability of 0.05, and increase the mortality rate of juveniles by 100% and adult mortality by 20%. These percentages are conservative; the actual mortality rates may be considerably higher, although the long-term values are unknown. Fitzpatrick and Woolfenden (1991) reduced adult survival to 0.55 and juvenile survival to 0.0 in their population model.

Promotion to next stage. Survivors of the mortality step are promoted to the appropriate "experienced" stage: novice breeders to experienced breeders; 1-year helpers to experienced helpers.

Dispersal. Two types of dispersal are modeled: *philopatric dispersal* - forays around the natal territory within an "assessment sphere", and *floater dispersal* - long distance search in which a disperser permanently leaves its area of intimate knowledge and moves through the landscape searching for breeder vacancies or empty territories.

All helpers that survive the mortality step engage in philopatric dispersal. The order in which philopatric dispersal events occur mirrors the dominance hierarchy of jays: males dominate females, older jays dominates younger, jays closer to their natal

territory dominate more distant jays. The first dispersal event allows male helpers to inherit their natal territory if both breeders have died. Male helpers then search their assessment sphere for unpaired females, and if successful they become novice breeders. Older males search before younger males to simulate dominance relations, and jays closer to their natal territory out compete more distant jays. Male helpers that fail to pair up then search for empty territories within their assessment sphere. Female helpers then search for unpaired males, and if unsuccessful search for empty territories, all within their assessment sphere. Mortality associated with these short distance forays is assumed to be already factored into the mortality rates for each stage.

Floater dispersal commences after philopatric dispersal; this ordering assumes that philopatric dispersers dominate floaters. Helpers of both sexes who were marked-to-disappear in the mortality step either die or leave their natal territory as floaters, depending on whether a random uniform deviate drawn for each helper exceeds the setting for the floater frequency parameter (see Table 5-1).

Searching behavior of floaters is modeled with several simple rules. Upon leaving the territory, the initial movement direction is random. As dispersers move through the landscape, they see territories or habitat within a user-specified detection radius. They process the objects they see in a specific order, first looking for breeder vacancies, then empty territories. If a breeder vacancy or empty territory is detected, the decision to settle is determined by the disperser's propensity to settle. If the disperser doesn't settle, it moves on towards the most attractive habitat that has not been visited already. In completely homogeneous habitat dispersers move in a straight line, but in non-homogeneous habitat their movement direction is affected by differences in habitat

attractiveness. They move away from habitat with low attractiveness, and towards habitat with high attractiveness. Dispersers remember previously visited locations, which makes it less likely that they will backtrack unless alternative directions are very unattractive.

Long distance dispersers have two mortality rates: one for dispersers within scrub, another for dispersers outside of scrub. Within scrub, the disperser survival rate is higher than outside of scrub (Table 5-1). Each disperser moves until it exceeds a random daily-distance-moved threshold selected for each jay from a distribution of daily move distances. Once the latter distance is exceeded, a daily mortality rate is used to determine if the jay survives to the next day. These steps are repeated for each jay until it dies, finds a mate or leaves the simulation area. Jays that leave the area are considered dead (i.e. there is no immigration from outside the simulation area). In contrast to short distant dispersers, long distance dispersers do not return home.

After all floaters have settled, died, or left the simulation area, the annual cycle is repeated with the reproduction step. If all jays are extinct or the last year of the last repetition is reached, the simulation terminates.

Territories

The model tracks individual territories, maintains a list of jays occupying each territory, and graphically displays the occupancy status of each territory. In the simulations completed for this project, all territories were assumed to be 9 hectares and shaped as squares. Territory locations were read in from an ASCII file exported from Arcview. Position, number, and habitat quality of territories did not change over time. All

territories were given parameter values for either high quality habitat or suburbs (see parameter settings in Table 5-1).

Background Landscape Image

Bit-mapped GIS files provided the landscape setting upon which the population dynamics and dispersal movements were simulated. These files were created by overlaying the scrub patches in the 1992-1993 SMP database onto a statewide habitat classification map produced by the Florida Game and Freshwater Fish Commission (FGFWFC) based on 1985-1989 Landsat Thematic Mapper data (Kautz et al. 1993). All GIS files had a spatial resolution of 30 m. The original landcover types coded in the FGFWFC classification are shown in Table 4-2 (chapter 4), along with the associated "attractiveness" values that affected the movement of floaters. In the simulations completed for this chapter, the landscape was assumed to be static through time.

Table 5-1. Demographic and dispersal parameter settings for jays in optimal and suburban conditions.

Parameter	Optimal conditions Female	Optimal conditions Male	Suburban conditions Female	Suburban conditions Male
Survival				
1st Year Helper	0.580[a]	0.740[a]	0.480[a]	0.480[a]
Older Helper	0.625[a]	0.740[a]	0.480[a]	0.480[a]
Novice Breeder	0.740	0.740	0.480	0.480
Experienced Breeder without Helper(s)	0.770	0.770	0.770	0.770
Experienced Breeder with Helper(s)	0.850	0.850	0.850	0.850
Fedundity				
Novice Breeder	0.50[b]		0.50[b]	
Experienced Breeder without Helper(s)	0.57 [b]		0.57 [b]	
Experienced Breeder with Helper(s)	0.77 [b]		0.77 [b]	
"Delay-and-foray" Dispersal				
Assessment sphere (radius – no. territories)	4	7	4	7
"Floater" Dispersal				
1st Year Helper – proportion disappearing jays becoming floaters	0.85	0.65	0.85	0.65
Older helper – proportion disappearing jays becoming floaters	0.85	0.65	0.85	0.65
Detection radius (meters)	450	450	450	450
Daily Survival in scrub	0.9988	0.9988	0.9988	0.9988
Daily Survival in non-scrub	K-M[c]	K-M[c]	K-M[c]	K-M[c]
Daily movement distance	Inverse[d]	Inverse[d]	Inverse[d]	Inverse[d]

a Includes disappearances (see chapter 4 for further explanation).
b Production of new 1st year helpers, not fledglings.
c Daily survival rates obtained from Kaplan-Meier curve (derived from radiotelemetry data - see chapter 4 for further explanation).
d Daily movement distances obtained from inverse function (derived from radiotelemetry data - see chapter 4 for further explanation).

Map Production

A statewide metapopulation map was produced to depict the 21 metapopulations that were analyzed for this chapter (Fig. 5 -1). For each of the 21 metapopulations, two types of detailed maps were produced to depict the status of jays in 1992-1993 as determined by the SMP, and to depict what jay populations might look like if all habitat were restored and fully occupied by jays. The maps showing restored populations of jays provided the basis for the simulations, as explained below.

Statewide metapopulation map

Metapopulations were delineated initially using a "dispersal buffer" approach discussed in chapter 2. A GIS was used to generate a 12 km buffer around all jay territories to enclose populations that are likely to be connected by dispersal. In certain areas the buffers joined populations that probably are not connected due to physical barriers to movement, such as a large river systems or cities. These physical barriers are identified in the written accounts for each metapopulation (see Metapopulation Viability Analysis section). Figure 5 -1 shows a map of the 21 metapopulations identified for the entire state. Each of these 21 metapopulations were modeled as demographically independent units as described below.

1992-1993 SMP maps

The status of jays and habitat as determined by the 1992–1993 SMP were portrayed for each metapopulation on one or more maps. The jay data included some

miscellaneous sightings added since 1993. The maps show habitat polygons shaded with coarse hatching representing different levels of human disturbance. Lightly shaded polygons delineate protected areas or areas proposed for protection/acquisition as of the end of 1997. These data were assembled from several agencies, and are now somewhat outdated. Protected areas containing scrub jays are labeled in italics. Thin, circular lines represent dispersal buffers connecting jay territories within 3 km of each other. A road network, county boundaries, and major cities also are depicted.

Acquisition maps

Acquisition maps show the jay territory locations used as input to the simulations. These maps show the estimated jay populations after habitat restoration and full occupancy. Three types of jays are delineated on the acquisition maps. Jays in currently protected habitat are enclosed in bold, solid polygons. The boundaries of the protected areas were estimated from 1997 information and some updated sources (see "Identification of Protected Areas" section below). Currently protected jays were included in all simulations. Jays in currently unprotected potentially suitable habitat are enclosed in bold, dashed polygons. These are the jays that may be included or excluded in different simulations, reflecting various reserve design options. Jays that are not enclosed in either type of polygon are considered to be "suburban" jays, and are included in all simulations. The polygons delineating groups of jay territories are labeled with alphanumeric identifiers consisting of a county-name prefix followed by an integer number (e.g. "Brev12"). These map labels are referred to in the text and tables to identify groups of jays. A road network, county boundaries, and major cities also are depicted.

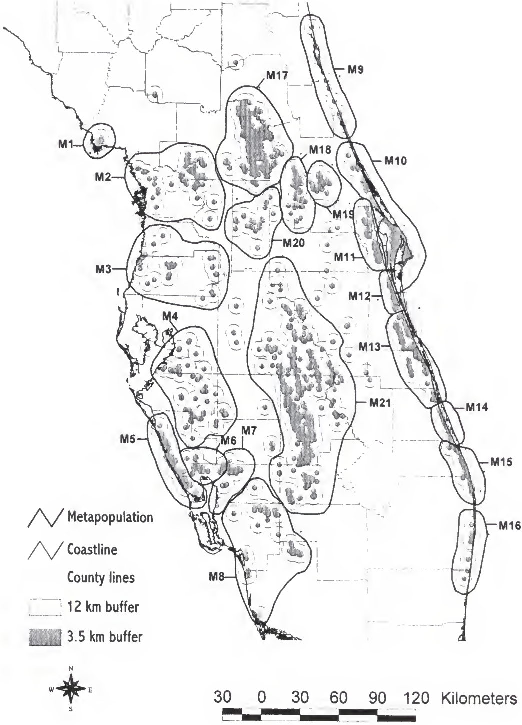


Fig. 5-0. Delineations of 21 Florida Scrub-Jay metapopulations based on 1992 - 1993 statewide survey.

GIS Database Preparation

Geographic information systems (Arc/Info, Arcview, and Imagine) were used to produce raster images of landscapes used in the simulations, to provide jay locations and territory quality information to the simulation model, and to produce maps described above.

Estimation of jay populations after restoration

The starting point for estimating jay population size for use in the simulations was the 1992-1993 SMP database produced at Archbold Biological Station in 1993 (Fitzpatrick et al. 1994), and subsequently updated by Bill Pranty, and now maintained by Archbold Biological Station (Reed Bowman). Additional jay locations were added to a copy of this database to reflect population sizes expected after habitat restoration and full occupancy by jays.

The number of jays expected to occupy patches after being fully restored was estimated by jay experts familiar with localities in the following counties: Jon Thaxton – S. Manatee, Sarasota, Charlotte, N. Lee; Dave Breininger and Brian Toland – Brevard, Indian River, St. Lucie, Martin; Grace Iverson – Palm Beach; Reed Bowman and Brad Stith – Highlands and Polk; Bill Pranty – Pasco, Hernando, Citrus, Lake, Marion. These experts were asked to examine maps showing the habitat patches and jay distributions from the 1992-1993 SMP, and to give a subjective estimate of the number of jays an area could support, based on their knowledge of the local conditions. In the remaining counties, an estimate was made by B. Stith based on habitat attributes in the SMP database, patch size, and supplemental habitat information where available (e.g. Pranty et

al. manuscript). Most of these estimates differed little from the densities determined by the SMP.

Identification of protected areas

Boundaries were digitized around occupied, protected jay habitat using Arcview. These boundaries appear on the acquisition maps for each metapopulation as heavy solid lines. Protected areas were identified through the use of the 1998 F.N.A.I. publication (Blanchard et al. 1998), annual C.A.R.L. reports (especially Anonymous 1999), Arc/Info coverages obtained from water management districts, and from verbal updates provided by individuals familiar with specific sites. The source data for the F.N.A.I. publication and the Arc/Info coverages date from late 1997. A significant number of acquisitions have been made since that time, some of which may not be identified as protected in this document. In a few cases, local experts suggested that a particular tract of land be treated as protected even though it was in private hands or the property had been only partially purchased. In these cases, it is possible that areas designated as protected may be less than shown on the maps. The ongoing process of land acquisition ensures that any map will be obsolete as soon as it is published, and such errors will affect the outcome of some simulations.

Assessment of unprotected areas

Unprotected, occupied patches of jay habitat delineated by the 1992-1993 SMP were grouped into two categories: patches having sufficient potential to be considered for acquisition, and patches with little or no acquisition value due to excessive human

disturbance (especially suburbanization). The determination of excessive degradation was made by local experts for the following counties: Jon Thaxton – S. Manatee, Sarasota, Charlotte, N. Lee; Dave Breininger and Brian Toland – Brevard, Indian River, St. Lucie, Martin; Grace Iverson – Palm Beach; Reed Bowman and Brad Stith – Highlands and Polk; Bill Pranty – Pasco, Hernando, Citrus, Lake, Marion. In the remaining counties, a determination was made by B. Stith based on habitat attributes in the SMP database and the density of road networks as portrayed in the Florida Atlas and Gazetteer (1997).

Potential jay habitat found to be unoccupied by the 1992-1993 SMP generally was not included in any of the modeling scenarios unless it was nearly adjacent to already occupied habitat. Manatee county was an exception to this rule due to the fact that the majority of patches in this area could not be surveyed during the SMP, and many patches are likely to be occupied. Note that patches found to be occupied in the early 1980's by Cox (1987) that were subsequently found to be unoccupied by the SMP were treated as unoccupied patches. Whether jays were added to an unoccupied patch can be ascertained by comparing the 1992-1993 SMP maps with the corresponding acquisition maps.

Suburban jays

Jays living in suburban conditions are unlikely to persist in the long term (Breininger 1999; Bowman et al. 1993). Nevertheless, suburban jays may play an important role in the short term by providing colonists to restored or well-managed habitat (Thaxton and Hingtgen 1996; Breininger 1999). To account for this potentially important role in the simulations, suburban jays were included in model runs for areas where they were originally present in the SMP. Suburban jays were assigned

demographic parameters corresponding to those measured by Breininger (1999) on Satellite Beach, Brevard County (table 5-1). Also, suburban jays were given different dispersal behavior compared to jays living in optimal habitat, based on the findings of Thaxton and Hingtgen (1996). Simulated jays dispersing from optimal habitat could not settle in suburban areas. Simulated jays from suburban areas could settle in optimal habitat, and could settle with unpaired jays in suburbs, but once a suburban territory became unoccupied, that territory could not be recolonized.

Simulation Runs

Each simulation run required two input files: a territory location/attribute file, and a background landscape file. The input files for all simulation runs are ASCII files exported from the Arcview database that was used to produce the acquisition maps for each metapopulation.

Repetitions and duration of simulations

All simulations were run for 30 repetitions. Statistics generated from 30 repetitions were found to stabilize and adequately represent much lengthier simulations. All simulations were run for a duration of 60 years. No standards currently exist for choosing the duration of simulations, but recent research shows a tendency towards shorter simulation times (Beissinger et al. 1998). The choice is arbitrary, and simulations run for different lengths of time commonly produce very different absolute outcomes; ultimately, all populations go extinct. However, relative outcomes are assumed to be the same; the ranking of relative risk of extinction faced by different populations remains unaffected by the length of the simulation (Beissinger et al. 1998).

Reserve design configurations

Two reserve design configurations played a key role in the analysis and comparison of scrub-jay metapopulations around the state. These two configurations, called the "no acquisition" and "maximal acquisition" options, represent the smallest and largest possible reserve designs. Both configurations were simulated for all metapopulations (except the Ocala National Forest).

The "no acquisition" option assumes that no more land will be acquired beyond what is currently protected. Jays outside protected areas are treated as suburban jays with the corresponding demographic characteristics (see table 5-1). The "maximum acquisition" option assumes that all relatively undisturbed habitat with jays will be acquired. For both configurations, all protected lands are assumed to be restored and properly managed for scrub-jays, and jays are assumed to have the appropriate densities and demographic performance for high quality habitat (see table 5-1).

Other configurations were simulated for metapopulations showing substantial differences between the "no acquisition" and "maximal acquisition" options. Typically, the very small and very large metapopulations did not warrant evaluating additional configurations because the results would be nearly the same as the two extreme configurations. For metapopulations where intermediate configurations might be substantially different, fixed percentages of jays were added to the already protected populations. The percentages (30% or 70%) were applied to the difference between the maximum and no acquisition option to determine the total size of the reserve.

In metapopulations with substantial spatial variability in unprotected jay distributions, alternative reserve designs were simulated that emphasized maximizing

territory contiguity (i.e. favoring larger areas), or maximizing connectivity (i.e. preserving small "stepping stone" populations).

Output statistics

Two main types of output statistics were generated by the model: quasi-extinction probabilities, and population trajectory statistics. A quasi-extinction curve was generated for each model run to show the cumulative probability (on the y-axis) that the population fell below a range of population sizes (on the x-axis) at any time during the simulation. Two statistics were extracted from each quasi-extinction curve: the probability of total extinction, and the probability of falling below 10 pairs (referred to throughout this document as the "quasi-extinction" probability). Prior research has identified a population size of 10 pairs as an important threshold for assessing vulnerability. These two statistics (extinction and quasi-extinction probability) were tabulated for all simulations, and provide useful information for evaluating populations that are highly vulnerable to extinction. Note that these two statistics do not provide any information about the viability of populations that never fall below 10 pairs.

To evaluate larger populations, the trajectory statistics are likely to be more useful than quasi-extinction statistics, as large populations may decline rapidly yet produce quasi-extinction statistics that indicate no risk. A population trajectory curve is generated for each model run which shows the mean population size (on the y-axis) for a given time period (on the x-axis). Several statistics were extracted from each trajectory curve: starting population size, mean ending population size, standard deviation, and percent population decline. Percent population decline is calculated by subtracting the mean

ending population size from the starting population size, dividing this difference by the starting population size, and multiplying this result by 100.

Model Validation/Calibration

Efforts to validate this model using long-term data from Archbold Biological Station (ABS) (Woolfenden and Fitzpatrick 1984) are described in chapter 4. The demographic parameters measured at ABS were used to parameterize jays in optimal habitat (table 5-1). A constraint analysis and a small radiotelemetry study (chapter 4) were used to develop parameters for the dispersal algorithm.

Interpreting Simulation Results

Two key assumptions have a large influence on the simulation results reported in this chapter. First, the assumption has been made that the density of jays in all occupied habitat is the maximum expected if the habitat were fully restored. The second assumption is that the demographic performance of jays is maximal, corresponding to measurements made in optimal habitat in the long-term study at Archbold Biological Station (Woolfenden and Fitzpatrick 1984). Both of these assumptions are likely to be very optimistic for most metapopulations around the state.

Many habitat patches, including those in public ownership, are not currently managed properly for scrub-jays. In the absence of aggressive management, jay demographic success decreases; small changes of 10% can produce dramatic declines in population size and rapid extinction (Fitzpatrick and Woolfenden 1986; Breininger 1998; Root 1998). The simulations results presented in this chapter assume continuous, optimal habitat conditions. Unfortunately, even proper management of habitat may not guarantee

demographic success, especially for patches that are juxtaposed against landscapes that subject jays to detrimental edge effects. These edge effects include human factors such as road mortality (Mumme et al., in press), and predation by domestic cats, and natural predators that occur at artificially high densities (e.g. racoons, grackles; Breininger 1999). More subtle edge effects may occur in “natural” landscapes where jay habitat is located next to forests or other habitats favorable to jay predators and competitors (Breininger et al. 1998).

It is likely that these negative factors, which depress jay densities and demographic performance, are the norm throughout much of the state. Fire management programs are being developed and implemented on many public lands, but as development continues in Florida many jays on these properties will have reduced reproductive success simply because they are surrounded by human landscapes. A recent study in well-managed jay habitat at Archbold Biological Station by Mumme et al. (in press) documented substantial negative effects of road mortality in a rural setting. The situation in suburban and urban settings is likely to be even worse (Breininger 1999; Bowman 1993). Because the simulation model does not consider such edge effects, the model results should be viewed as optimistic.

Given these caveats, the recommended use of the estimates reported below is to compare the relative viability of jay metapopulations around the state as a guide for land acquisition and to rank areas in terms of vulnerability. Probability and trajectory estimates produced by the model should not be taken literally; they are best used for comparative purposes.

Results

These results summarize the output of different simulations performed for each of the 21 metapopulations. Results for each metapopulation are reported in separate sections. Each section begins with a general description, lists the protected areas, discusses restoration potential, summarizes the simulation results, and provides recommendations. Maps are provided showing the distribution of jays and habitat during the 1992-1993 SMP, and the distribution of jays in relation to the simulations and acquisition possibilities. The acquisition maps depict what jay populations might look like if all habitat were restored and fully occupied by jays. Tables are provided that summarize the patch statistics (number of jays in each patch) for different reserve configurations. The results from all simulations are presented in tables, and quasi-extinction and trajectory graphs are provided for at least 2 reserve design configurations. The simulation results also include the statewide rankings developed and explained in the last section (see "Recommendations").

Levy (Cedar Key) (M1)

General description: The Levy county metapopulation is the most northerly population of jays occurring along the Gulf Coast, and is highly isolated from other metapopulations. The SMP delineated a single large scrub patch in this area, and found 8 groups of jays, 4 of which occurred in the Cedar Key Scrub State Reserve (see Fig. 5-1a; Table 5-1a). The SMP found the condition of the scrub to be severely overgrown, and noted that the number of jays present was only one-third the number found by Cox in 1980 (Pranty et al. manuscript). A 1997-1998 study of jays at Cedar Key (T. Webber in F.D.E.P. 1998) found only 1 pair on the reserve, 2 pairs in a nearby junkyard, and 4 groups in the town of Rosewood 7-8 miles to the east. Estimated potential population size after habitat restoration and full occupancy is 17 pairs in currently protected areas, and 75 pairs maximum.

Protected areas: The only protected jays in this metapopulation occur in the Cedar Key Scrub State Reserve ("Levy1").

Restoration potential: Some restoration has taken place at the Cedar Key Scrub State Reserve, but many areas remain heavily overgrown. A recent report (F.D.E.P. 1998) noted that a shortage of staff and difficulties associated with burning sand pine forests have delayed restoration needed at this reserve. For modeling purposes, the currently protected area is estimated to support about 17 jay families after restoration and full occupancy (Fig. 5-1b; Table 5-1a). A large, contiguous patch of unprotected habitat ("Levy2") was mapped by the SMP, but much of this habitat is not suitable for jays. Restorable patches of scrub and scrubby flatwoods occur within a complex matrix of

marsh and mesic flatwoods with high densities of pine. The estimated population sizes after restoration (Table 5-1a) may be overly optimistic.

Simulation results: This metapopulation ranked 5th in vulnerability (table 5-23), 17th in percent protected (22.7%; table 5-24), and 2nd in priority (table 5-25), with high vulnerability and high potential for improvement. Simulations of the SMP configuration indicate that the 1992-1993 configuration is extremely vulnerable to extinction (Table 5-1b; extinction risk = 1.0; percent population decline = 100.0).

Simulations of the currently protected, restored configuration indicate that the protected population would be vulnerable to extinction (Table 5-1b; extinction risk = 0.1; Fig. 5-1d; percent population decline = 29.4%).

Because the habitat as mapped shows no fragmentation, no configurations involving multiple patches were simulated. All acquisition configurations assume that preference is given to acquiring contiguous habitat, but even if multiple patches were created, the resulting interpatch distances would be small.

The 30% acquisition configuration was estimated to support about 34 jay families (Table 5-1a). Simulations of this configuration indicate that it has a small but significant probability of falling below 10 families (Table 5-1b; quasi-extinction = 0.05). The mean population trajectory shows an 8.8% decline.

The 70% acquisition configuration was estimated to support about 54 jay families. Simulations of this configuration indicate that the population would not be vulnerable to extinction or quasi-extinction (Table 5-1b and Fig. 5-1d; extinction risk = 0.0; quasi-extinction = 0.0). The mean population trajectory shows a 3.7% decline (Fig. 5-1c).

The maximum acquisition configuration was estimated to support about 75 jay families. Simulations of this configuration indicate that the population would not be vulnerable to extinction or quasi-extinction (Table 5-1b; Fig. 5-1d; extinction risk = 0.0; quasi-extinction = 0.0; percent decline = 1.3).

Recommendations: Jays in this metapopulation are in a very precarious state, and their #2 priority rating perhaps should be upgraded to #1. Only one pair of jays is known to occur within the park, and only two other pairs are nearby (T. Webber in F.D.E.P. 1998) and these jays are subject to predation by cats and mortality along increasingly busy roads. A much greater level of support is needed to bolster current restoration efforts. The simulation results suggest that even after full restoration, additional land purchases beyond 30% are needed to reduce quasi-extinction risk to a low level. The opportunity may still exist to acquire substantial pieces of unprotected habitat adjacent to or near the Cedar Key Scrub State Reserve, but new housing developments are rapidly destroying habitat along SR 24 and CR 347, and acquisition opportunities may soon be foreclosed. Major efforts will be needed to restore any habitat that is acquired; removal of extensive pine overstory will be needed in many areas. This metapopulation is in danger of blinking out, and needs immediate attention.

Fig. 5-1a. Levy county map – 1992 - 1993 jay and habitat distribution.

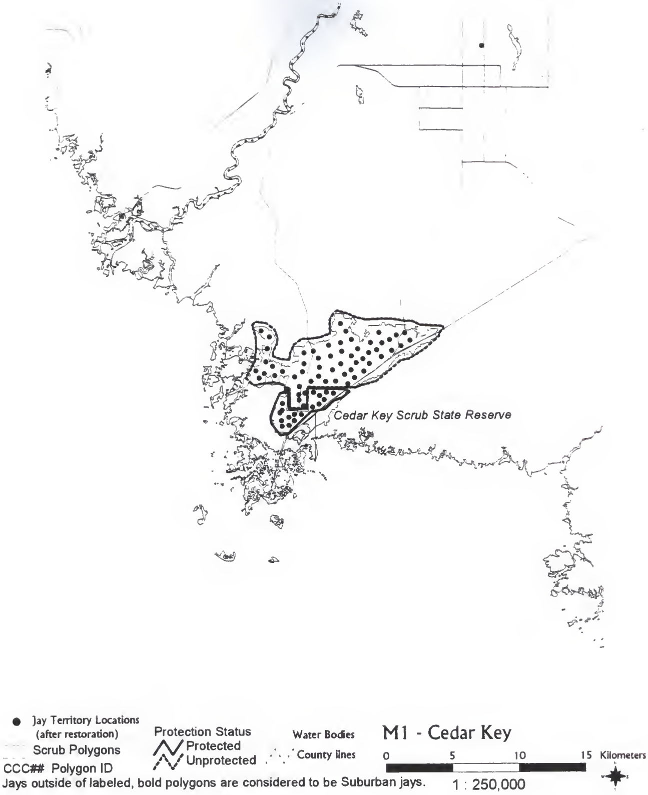
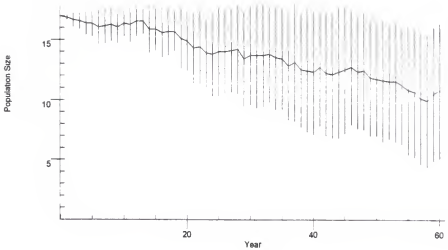


Fig. 5-1b. Levy county acquisition map.

Table 5-1a. Levy county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	30% preserved by contiguity	70% preserved by contiguity	Maximum acquisition
Levy1	Cedar Key Scrub Reserve	4	17	17	17	17
Levy2		4		17	37	58
Totals		8	17	34	54	75



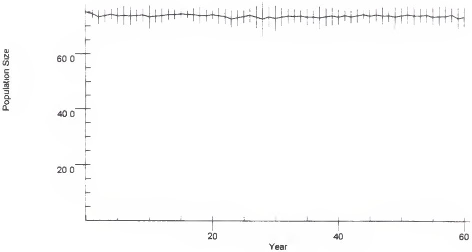
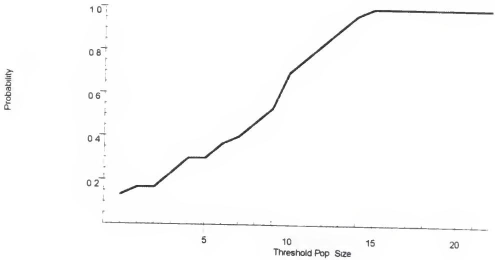


Fig. 5-1c. Levy county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



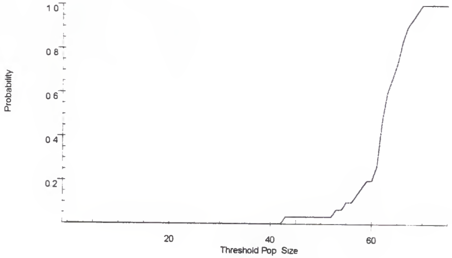


Fig. 5-1d. Levy county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-1b. Levy county (Cedar Key) simulation statistics

Patch Name	Data type	Original 1992-1993 scenario	No acquisition	30% acquisition by area	70% acquisition by area	Maximum acquisition
Cedar Key Scrub Reserve	starting population size	4	17	34	54	75
	x end pop. size ± s.d.	0 0.8	12 5	31 6	52 5	74 5
	percent decline	100.0	29.4	8.8	3.7	1.3
	extinction risk	1.0	0.1	0 (8)	0 (26)	0 (45)
	quasi-extinction risk (10 pairs)	--	0.82	0.05	0	0

Citrus-S.W. Marion (M2)

General description: The Citrus and S.W. Marion county metapopulation consists of small, scattered groups of jays living within about ten miles of the Gulf Coast, and larger populations of jays concentrated mostly in the Big Scrub area of southwest Marion and northwest Sumter counties. Most jays occur in small, somewhat isolated clusters; the largest population is an unprotected group of 19 pairs at "Mar2" (fig. 5-2b). Extensive mosaics of scrub, scrubby flatwoods, sand pine, and sandhill occur throughout this region. The habitat as mapped by the SMP makes no distinction among habitat types and should be treated as very incomplete. Because of the severely overgrown habitat conditions, many jays occur in marginal habitat, and the small, isolated populations along the Gulf Coast are especially vulnerable to blinking out. The connection between the Gulf Coast and Big Scrub area may be very poor; the 12 km dispersal buffer (fig. 5-1) shows the tenuous connection occurring at the Twisted Oak golf course ("Citr5" in fig. 5-2b). The SMP documented about 108 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 47 pairs in currently protected areas, and 145 pairs maximum.

Protected areas: The only protected jays along the coastal portion of this metapopulation occur at the Crystal River State Buffer Preserve ("Citr1"). Protected jays inland occur at Potts Preserve ("Citr6"), Cross Florida Greenway ("Mar1", "Mar5", "Mar6"), and Half Moon Wildlife Management Area ("Sumt1"). CARL sites with jays include "Mar8".

Restoration potential: Nearly all of the habitat in this metapopulation is heavily overgrown and occurs as a complex mosaic of scrub, scrubby flatwoods, sandhill and

sandpine. Most of the larger habitat polygons mapped by the SMP include large amounts of non-habitat, and the data are inadequate for making good estimates of restoration potential. For modeling purposes, the only habitat polygon that was given significantly more jays after restoration is the Crystal River State Buffer Preserve. Jays in the large polygons in southwest Marion were kept at the densities determined by the SMP, which may significantly underestimate the restoration potential.

Simulation results: This metapopulation ranked 13th in vulnerability (table 5-23), 13th in percent protected (37.6%; table 5-24), and 8th in priority (table 5-25), with high vulnerability and moderate potential for improvement. No simulations were run for the SMP configuration due to its similarity to the "70% connectivity" configuration (see results in Table 5-2b).

The fully restored, currently protected configuration was estimated to support 47 jay pairs. Simulations of this "no acquisition" configuration indicate that the metapopulation would be vulnerable to extinction and quasi-extinction (Table 5-2b; extinction risk = 0.17; quasi-extinction risk=0.47; % decline = 78%).

All intermediate simulations, except the "70% preserved by area" configuration, show a non-zero extinction probability and significant quasi-extinction risk (Table 5-2b). Simulations of the latter configuration and the "maximum acquisition" configuration both show a small quasi-extinction risk (Table 5-2b). The percent population decline is fairly large for both configurations, reflecting the vulnerability of relatively small, somewhat isolated subpopulations.

Recommendations: Improved habitat mapping is needed to better estimate the restoration potential of the existing habitat. Additional surveys may be warranted

throughout this region, since jays often occur in atypical, unsurveyed habitat, as evidenced by the recent discovery of jays at Marion 1, Ross Prairie and in "Citr3" during surveys for the proposed Suncoast Parkway II.

The restoration potential in this region is probably considerably higher than reported here due to poor habitat data—considerably more habitat exists than is shown on these maps. Because no large, contiguous populations of jays occur in this metapopulation, even the "maximum acquisition" option is vulnerable to quasi-extinction and shows a large mean percent population decline. These simulation results suggest that as much habitat should be acquired and restored as possible, with an emphasis on creating larger contiguous populations. Extensive areas of overgrown upland habitat exists throughout both counties, and acquisition/restoration of parcels of unoccupied habitat may be needed to attract jays in suboptimal habitat to restored habitat, especially in Citrus county. A large sandpine forest occurs in N. central Citrus county with some logged areas that may now be suitable for at least 5-25 jay territories (B.Stith pers. obs. – see intersection of "Citr3" with this habitat polygon in fig. 5-2b). The feasibility of acquiring and restoring portions of this large forest should be investigated. Jays occurring along the powerline corridor of the Crystal River nuclear power plant ("Citr3") might recolonize this patch.

Recent additions to the Crystal River State Buffer Preserve ("Citr1" in fig. 2-2b) have increased the amount of protected scrub to nearly 400 acres (pers. comm. Randy Martin), making this the most significant habitat patch along the Gulf Coast portion of this metapopulation. Rapid restoration of this patch is crucial, as there may only be one or two jay families persisting at this site (B.Stith pers. obs.). "Citr5" (Twisted Oak golf

course) may be a potentially important "stepping stone", and a local reserve at this site should be considered.

In the Big Scrub area of S.W. Marion, large populations of unprotected jays occurs near Gum Slough ("Mar2") on the Rocking F Ranch, and just north of the Cross Florida Greenway on the west side of I-75 in the vicinity of the Marion Oaks D.R.I. ("Mar8"). Acquisition and restoration of these patches is especially important to the overall persistence of this jay metapopulation.

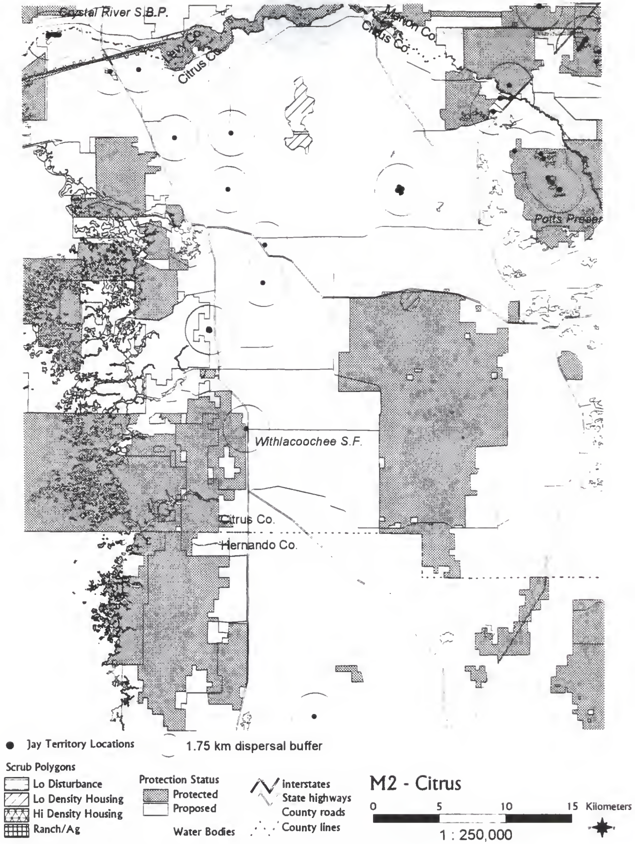


Fig. 5-2a. Citrus county map – 1992-1993 jay and habitat distribution.

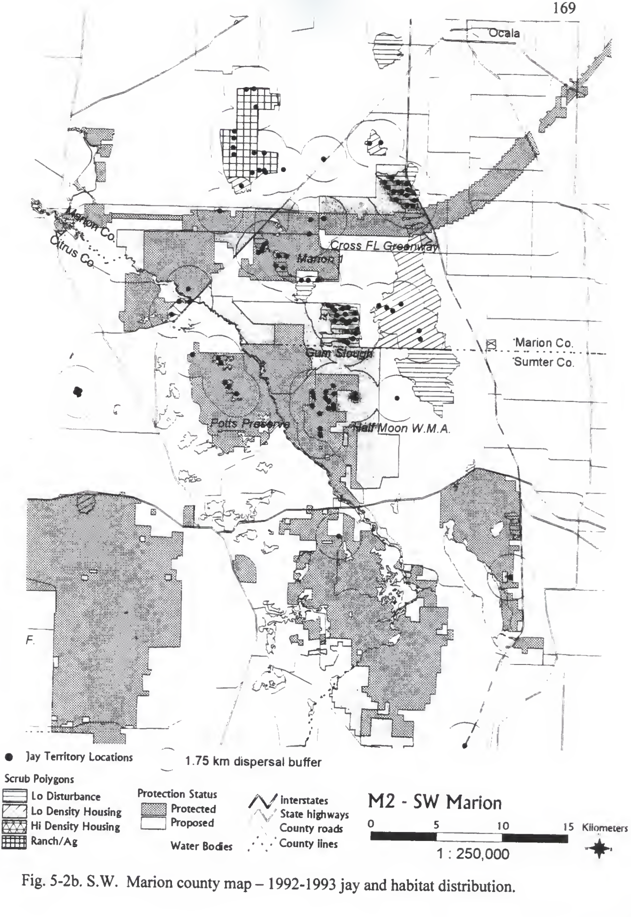


Fig. 5-2b. S.W. Marion county map – 1992-1993 jay and habitat distribution.

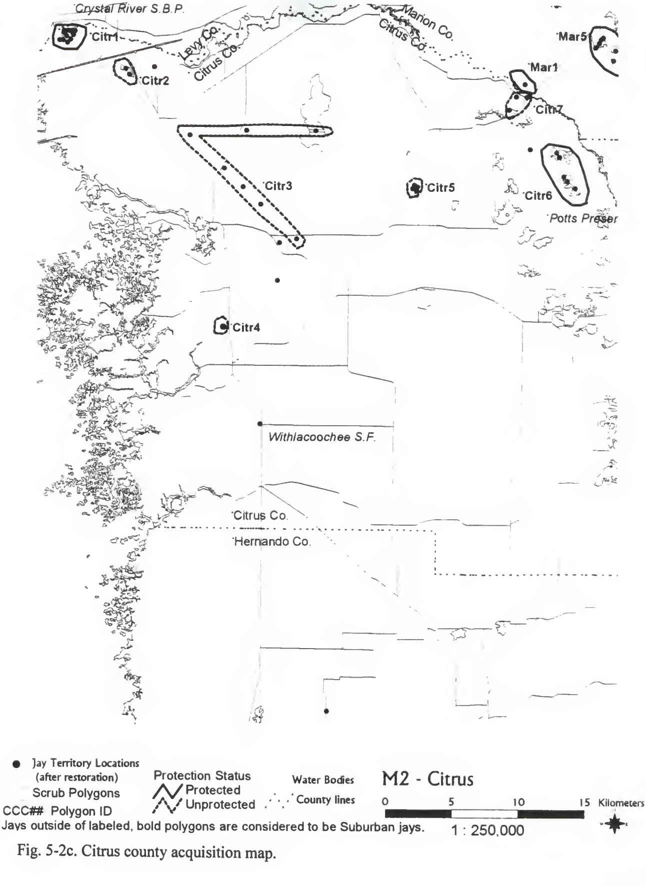


Fig. 5-2c. Citrus county acquisition map.

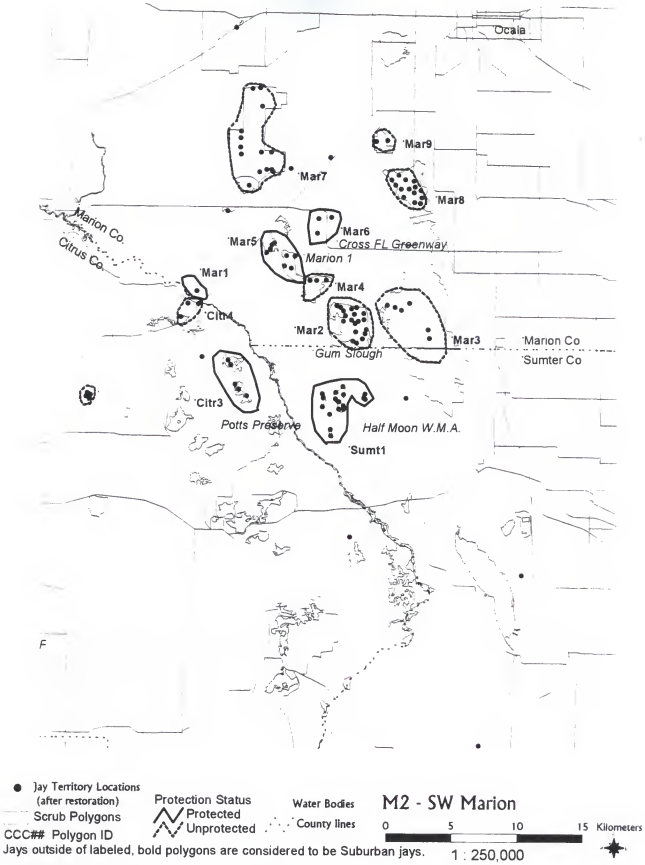
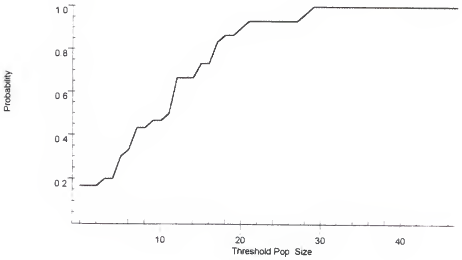


Fig. 5-2d. S.W. Marion county acquisition map.

Table 5-2a. Citrus and S. Marion county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	30% preserved by contiguity	30% preserved by connectivity	70% preserved by contiguity	70% preserved by connectivity	Maximum acquisition
Citr1	Crystal River St. Buf. Pr.	6	12	12	12	12	12	12
Citr 2		1		2	1	2	2	2
Citr 3		3			6		7	7
Citr 4		4			2	4	4	4
Citr 5		4			2		2	4
Citr 6	Potts Preserve	1	6	6	6	6	6	6
Citr 7		3					3	3
Mar1	Cross Fl. Greenway		1	1	1	1	1	1
Mar2		19		10	5	19	12	19
Mar3		6			1	4	4	6
Mar4		3		3		3	3	3
Mar5	Cross Fl. Greenway	8	8	8	8	8	8	8
Mar6	Cross Fl. Greenway	3	3	3	3	3	3	3
Mar7		14			3	6	11	14
Mar8		14		7	2	14	10	14
Mar9		2				2	2	2
Sumt1	Half Moon W.M.A.	17	17	17	17	17	17	17
Totals		108	47	69	69	101	101	125



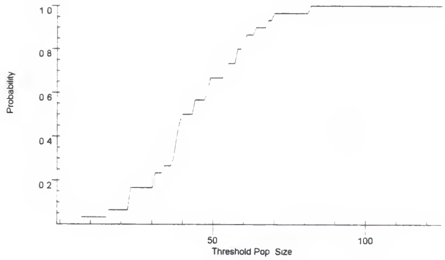
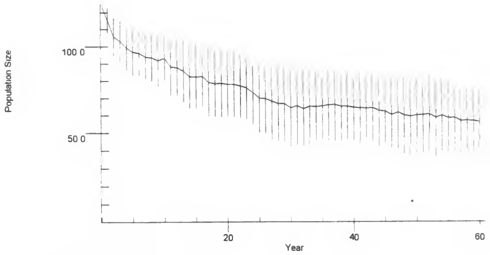


Fig. 5-2e. Citrus and S. Marion county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



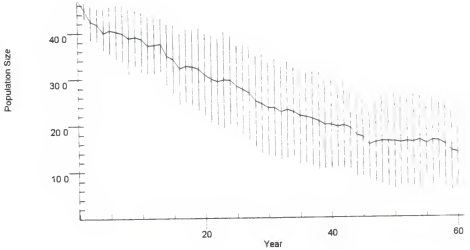


Fig. 5-2f. Citrus and S. Marion county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition

Table 5-2b. Citrus and S. Marion county simulation statistics

Data type	No acquisition	30% preserved by connectivity	30% preserved by area	70% preserved by connectivity	70% preserved by area	Maximum acquisition
starting population size	47	69	69	101	101	125
x end pop. size ± s.d.	13.8 8.5	15.0 11.4	24.4 16.1	32.7 20.1	48.3 20.1	56.2 17.7
percent decline	70.6	78.3	65.2	67.6	52.2	55.0
extinction risk	0.17	0.10	0.03	0.03	0.05	0.04
quasi-extinction risk (10 pairs)	0.47	0.57	0.43	0.17	0.27	0.0

Pasco-Hernando (M3)

General description: The Pasco-Hernando metapopulation (M3) consists of several poorly connected subpopulations that occur near the coast, in the interior of Pasco, and on the western edge of the Green Swamp. The SMP documented about 29 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 63 pairs in currently protected areas, and 69 pairs maximum.

Protected areas: This metapopulation ranked very high (3rd) in percentage of jays protected. However, many unprotected areas are poorly surveyed (see below). Protected jays have been found at: Weeki Wachee ("Her1"), Starkey & Serenova Wellfield ("Pas1"), Cross-Bar Wellfield ("Pas3)", Alston Tract ("Pas5"), Green Swamp W.M.A. ("Pas6").

Restoration potential: The restoration potential of this metapopulation is large (compare first and last data columns in Table 5-3a), especially at Weeki-Watchee ("Her1") and the Cross-bar/Al-bar Wellfields area ("Pas3", "Pas4").

Simulation results: This metapopulation ranked 14th in vulnerability (table 5-23), 3rd in percent protected (91.3%; table 5-24), and 11th in priority (table 5-25), with high vulnerability and moderate potential for improvement.

Simulations of the SMP configuration, with 20 jay families, indicated that this configuration is extremely vulnerable to extinction (Table 5-3a; extinction risk = 1.0).

The "no acquisition" configuration was estimated to support about 63 jay families after restoration and full occupancy. Simulations of the currently protected, restored configuration showed a small quasi-extinction risk (p=0.03) and a substantial quasi-

extinction risk ($p=0.30$; Table 5-3b). The maximum acquisition configuration, estimated to support only 6 additional jay pairs (total of 69), had no extinction risk and a reduced quasi-extinction risk ($p=0.233$).

Recommendations: The Pasco-Hernando metapopulation should be considered poorly surveyed; fire suppression has forced jays to occupy atypical, unsurveyed habitat, as evidenced by the recent discovery of jays at "Pas2" (Pranty et al., manuscript). This small population connects the 12 km dispersal buffer between Cross-bar and Serenova, and may be an important acquisition. In the absence of new survey data, further acquisition options appear very limited.

The potential for restoration of protected habitat in this metapopulation is large. The Weeki Watchee State Park ("Her1" in Fig. 5-3b) is a large sand pine forest with a dense oak understory that has had a single resident jay family residing in a small burn for many years. This forest has the potential to support 17 or more pairs of jays, but the one resident family may have recently disappeared (Pranty et al., manuscript). Portions of this forest should be restored to scrub as soon as possible. The largest population of jays in this metapopulation, and perhaps the 2nd largest jay population along the Gulf Coast, occurs on the Cross-bar/Al-bar Wellfields ("Pas3"), which is currently being restored by Pasco county (B. Pranty, pers. comm.). Habitat restoration is urgently needed at the Starkey and Serenova properties ("Pas1"), as jays are nearly extirpated at this site.

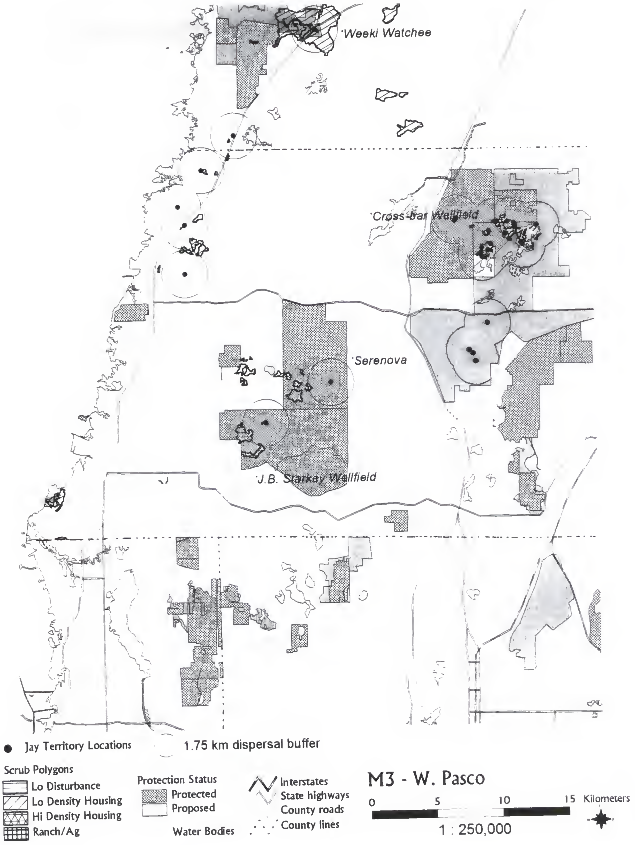


Fig. 5-3a. W. Pasco and Hernando county map – 1992 – 1993 jay and habitat distribution.

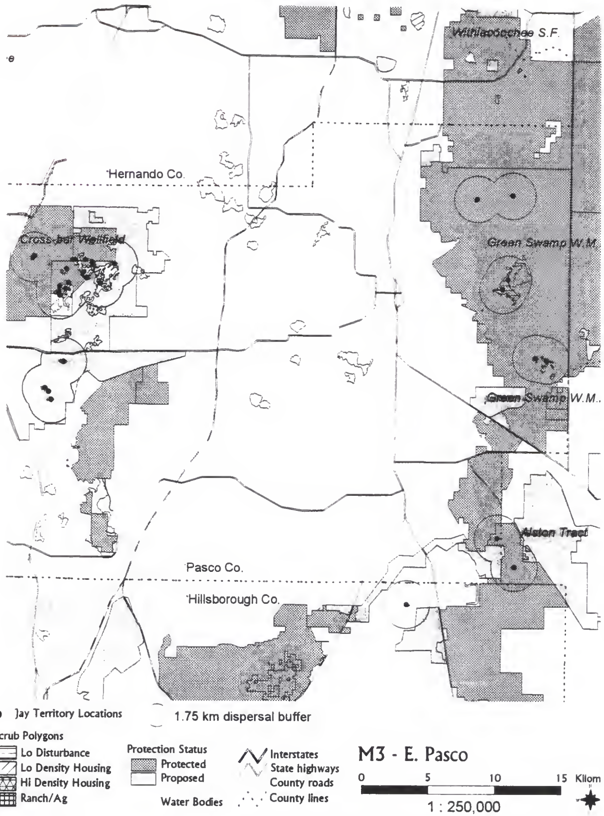


Fig. 5-3b. E. Pasco and Hernando county map – 1992 – 1993 jay and habitat distribution.

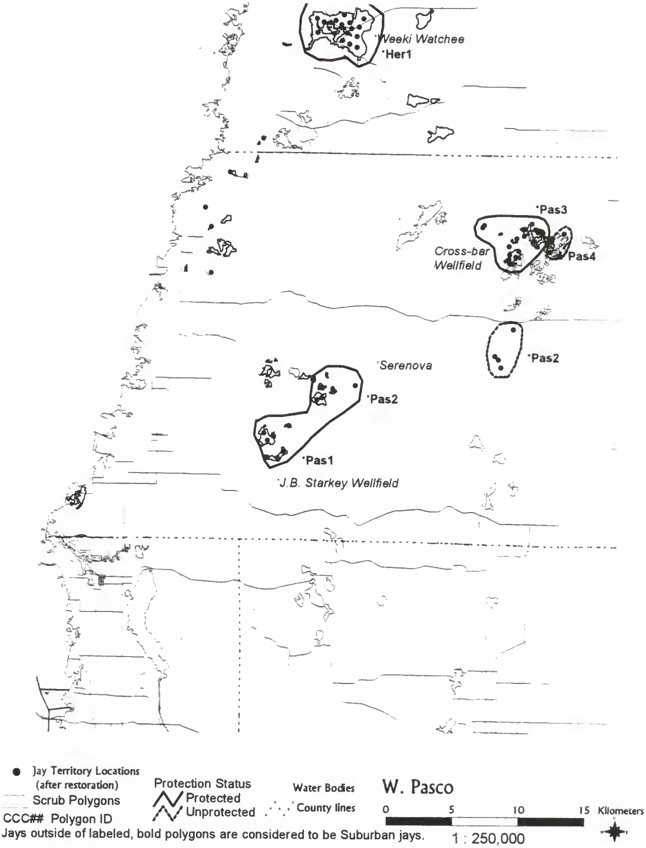


Fig. 5-3c. W. Pasco and Hernando county acquisition map.

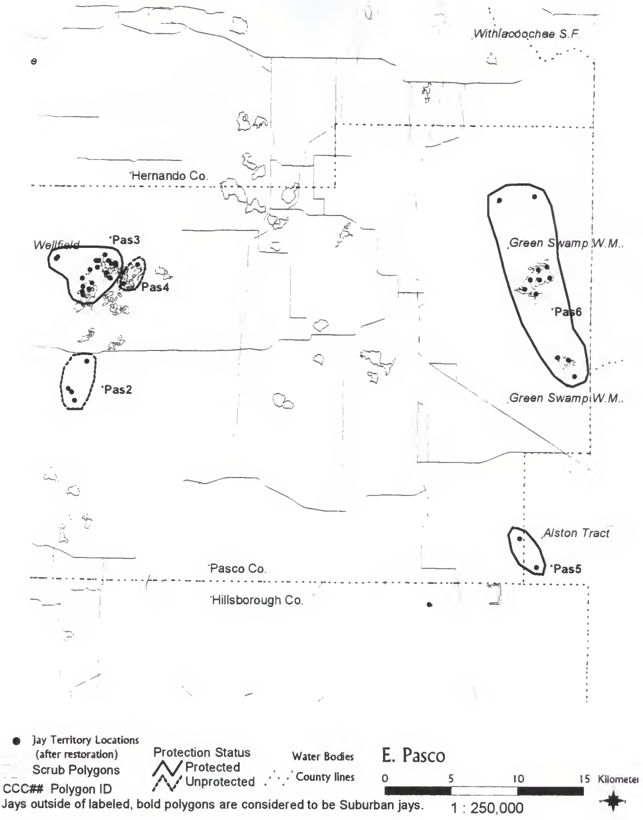
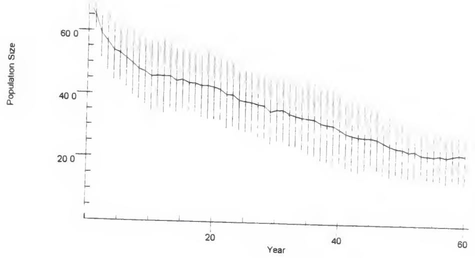


Fig. 5-3d. E. Pasco and Hernando county acquisition map.

Table 5-3a. Pasco and Hernando county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	Maximum acquisition
Her1	Weeki Wachee	1	17	17
Pas1	Starkey Wellfield & Serenova	3	13	13
Pas2				4
Pas3	Cross-Bar/Al-bar Wellfield	15	19	19
Pas4		2		2
Pas5	Alston Tract	2	2	2
Pas6	Green Swamp W.M.A.	6	12	12
Totals		29	63	69



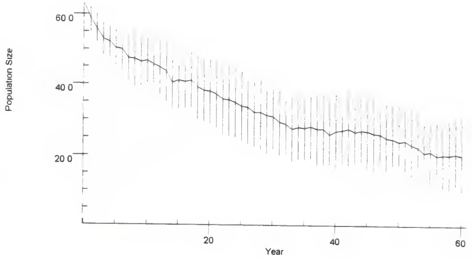
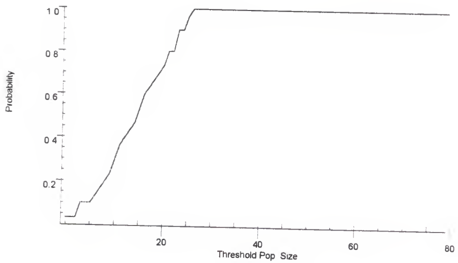


Fig. 5-3e. Pasco and Hernando county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



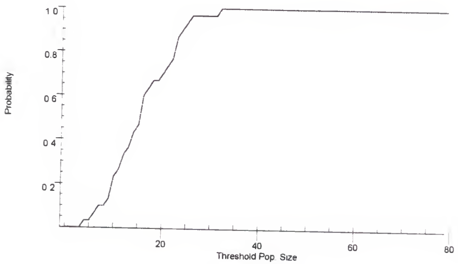


Fig. 5-3f. Pasco and Hernando county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-3b. Pasco county simulation statistics

Data type	1992-1993	No acquisition	Maximum acquisition
starting population size	29	63	69
x end pop. size ± s.d.	6.2 4.5	20.2 10.5	22.0
percent decline	78.6	67.9	68.2
extinction risk	0.23	0.03	0.0
quasi-extinction risk (10 pairs)	0.97	0.30	0.233

Manatee-S. Hillsborough (M4)

General description: This metapopulation occurs predominantly in Manatee and S. Hillsborough counties, with a few jays occurring in west Hardee and northeast Sarasota county. The configuration of habitat in this region as mapped by the SMP is very unusual, occurring as small patches isolated from each other by small to moderate distances (1 – 10 km). During the 1992-1993 survey, a significant number of patches were on private lands that could not be accessed. The SMP documented about 65 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 36 pairs in currently protected areas, and 145 pairs maximum.

Protected areas: Golden Aster Scrub Nature Preserve ("Hill9"), Balm-Boyette Scrub ("Hill8"), Little Manatee River ("Hill2"), Little Manatee River State Recreation Area ("Hill3"), Duette Park ("Man15"), Lake Manatee Lower Watershed ("Man10"), Beker ("Man12", "Man16"), Lake Manatee State Recreation Area ("Man17"), Myakka River State Park ("Sar15"), Verna Wellfield ("Sar19").

Restoration potential: Many of the patches in this metapopulation are heavily overgrown, but the restoration potential of the numerous small patches may not be much greater than the SMP population estimates. Nevertheless, habitat restoration is urgently needed in many of the protected areas, since local populations of jays are small and very vulnerable to local extinction.

Simulation results: This metapopulation ranked 6th in vulnerability (table 5-23), 14th in percent protected (24.8%; table 5-24), and 10th in priority (table 5-25), with high vulnerability and moderate potential for improvement.

After restoration, the "no acquisition" configuration was estimated to support about 36 jay territories in existing protected areas. This configuration had a very high risk of extinction (p=0.97) and quasi-extinction (p=1.0).

Simulations for this metapopulation produced unexpected results that were strikingly different from all other metapopulations. All scenarios for this metapopulation declined rapidly and had high extinction and quasi-extinction risk. Even the "maximum acquisition" configuration, with 145 pairs, had an extinction risk of 0.30, and a quasi-extinction risk of 0.90 (Table 5-4b).

These results are rather surprising. The model predicts that the long-term probability of persistence is low for all configurations, yet there is no doubt that jays have persisted in this area for many decades. Several factors may account for this apparent discrepancy. First, this was the least thoroughly surveyed metapopulation; more than 67% of the patches were inaccessible. Undoubtedly, many more jays occur in this area than were found during the SMP. For modeling purposes, some jays were added to unsurveyed patches (compare Figs. 5-4a & b), but at lower densities than surveyed areas (this was the only metapopulation in which substantial number of jays were added to unsurveyed or unoccupied patches). Second, many jays probably occur in atypical habitat that could not be identified on soil maps or aerial photographs used for the SMP. This is evidenced by the recent discovery of jays in the northeast portion of this metapopulation (R. Bowman, pers. comm.). Third, significant portions of the jay habitat in this area may have been modified or lost recently (during the last couple of decades) due to vegetable farms and ranch activities. Cox (1987) mentions records of abundant jays in Manatee county along the coast which disappeared due to suburban development (e.g. near

Bradenton). Displacement of jays from developing areas and lags in population decline are likely; model predictions of substantial declines in jay populations may be reasonable, given the current landscape. Fourth, the habitat matrix may be less hostile to dispersers than the model assumes. Many of the habitat patches occur in ranch settings with a fairly open matrix and little or no suburbanization, which may create favorable conditions for floater dispersal. However, simulations conducted by Stith et al. (manuscript in prep.) suggest that even with unrealistically high floater dispersal ability and survivorship, jays are unlikely to survive long-term in landscapes with small, somewhat isolated patches unless landscape features such as corridors direct the movement of floaters towards occupied patches.

Recommendations: A more comprehensive survey for jays is needed to fill in the large data gaps. Besides mapping unsurveyed scrub patches, special effort should be made to map atypical habitats with low densities of oak scrubs, as these may be important to jays in this metapopulation. Clusters of contiguous jay territories are conspicuously absent in this landscape. Acquisition efforts should emphasize larger patches that are as close as possible to other large patches. Unprotected, unsurveyed patches near the north ("Man16") and south ("Man15") section of Beker, and further south at "Man9", Man10", Man11", and "Man5"are likely candidates. Acquisition of "Sar16" and "Man1", which are near protected jays at Verna Wellfield ("Sar19") and Myakka River State Park ("Sar15") would benefit these jays. Besides restoring overgrown scrub, habitat management should seek to remove dispersal barriers between patches. Creation of partially cleared right-of-ways between patches may facilitate dispersal (research on this subject is needed).

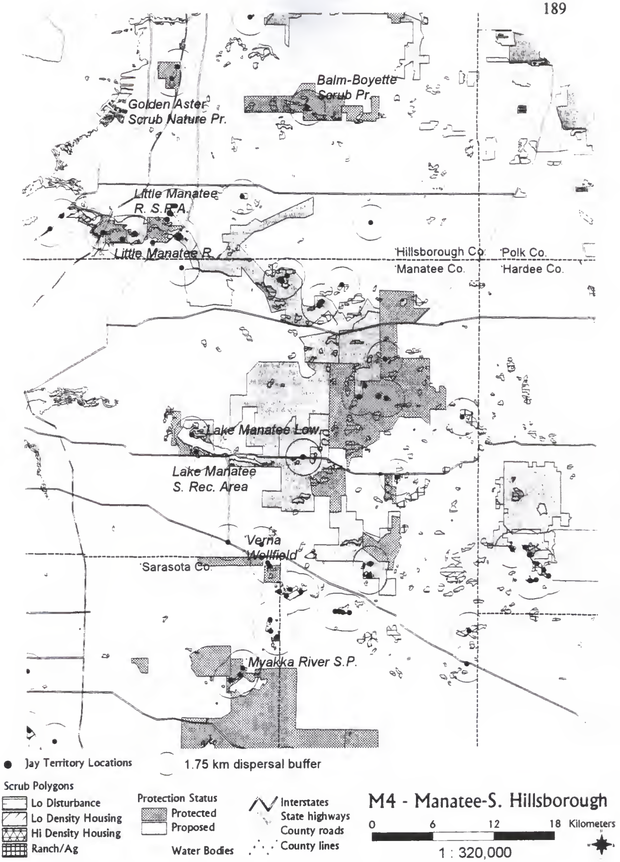


Fig. 5-4a. Manatee and S. Hillsborough county map – 1992 - 1993 jay and habitat distribution.

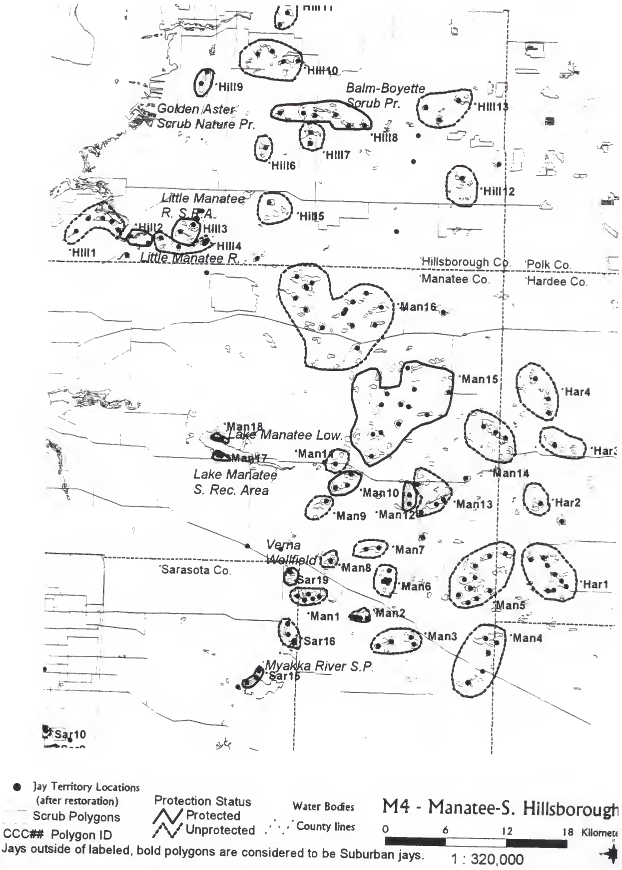


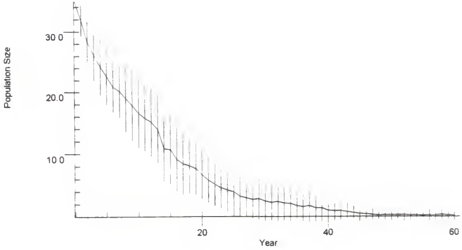
Fig. 5-4b. Manatee and S. Hillsborough county acquisition map.

Table 5-4a. Manatee and S. Hillsborough county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	30% preserved by contiguity	30% preserved by connectivity	70% preserved by contiguity	70% preserved by connectivity	Maximum acquisition
Har1		8			3	8	8	8
Har 2								1
Har 3								1
Har 4					4		2	3
Hill1		2				3	2	5
Hill2	Little Manatee R.	2	2	2	2	2	2	2
Hill3	Little Manatee R. S. Rec. Area	1	2	2	2	2	2	2
Hill4		8			3	8	8	8
Hill5		1			1	1	1	1
Hill6								1
Hill7						2		2
Hill8	Balm-Boyette Scrub Pr.	1	6	6	6	6	6	6
Hill9	Golden Aster Scrub Nature Pr.	2	2	2	2	2	2	2
Hill10								4
Hill11		2				2	2	2
Hill12								1
Hill13								3
Man1		4		5	3	5	5	5
Man2		4		4	2	4	4	4
Man3							3	5
Man4		3			2	5	5	5
Man5					1	6	5	10
Man6		2		5	3	5	3	5
Man7								2

Table 5-4a continued.

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	30% preserved by contiguity	30% preserved by connectivity	70% preserved by contiguity	70% preserved by connectivity	Maximum acquisition
Man8								1
Man9								1
Man10	Lake Manatee Lower Watershed		3	3	3	3	3	3
Man11		1			1	1	1	2
Man12	Beker		2	2	2	2	2	2
Man13		1			1	4	4	4
Man14		1			1		1	3
Man15	Duette Park	6	11	11	11	11	12	12
Man16	Beker	6		8	6	15	15	15
Man17	Lake Manatee St. Rec. Area	1	2		2	2	2	2
Man18		1			1	3	3	3
Sar15	Myakka River St. Pk.	3	3		3	3	3	3
Sar16		3			2	4	4	4
Sar17		2	2		2	2	2	2
Totals		65	36	69	69	112	112	145



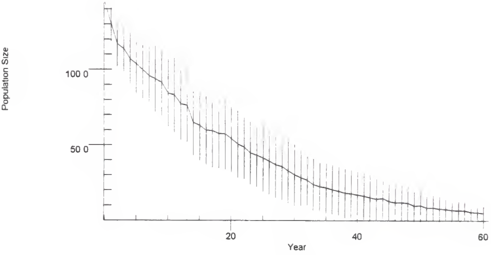
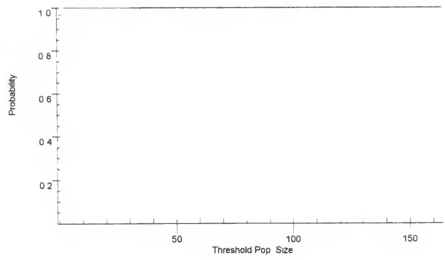


Fig. 5-4c. Manatee and S. Hillsborough county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



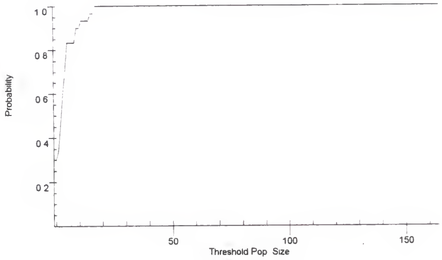


Fig. 5-4d. Manatee and S. Hillsborough county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-4b. Manatee and S. Hillsborough county simulation statistics

Data type	No acquisition	70% acquisition by connectivity	70% acquisition by area	Maximum acquisition
starting population size	36	112	112	145
x end pop. size ± s.d.	0.2 0.7	5.5 8.2	2.4 4.0	4.9 4.6
percent decline	95.3			96.6
extinction risk	0.97	0.43	0.60	0.30
quasi-extinction risk (10 pairs)	1.0	0.90	0.97	0.90

Sarasota-W. Charlotte (M5)

General description: The Sarasota-W. Charlotte metapopulation occurs along the Gulf coast from central Sarasota county south into Charlotte county, terminating at Charlotte Harbor. It is separated from the N.W. Charlotte county metapopulation by the Myakka River. The largest single population of jays along the Gulf coast occurs here in Oscar Sherer State Park. The SMP documented about 64 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 50 pairs in currently protected areas, and 89 pairs maximum.

Protected areas: Only two protected areas have the potential to protect more than 10 pairs of jays: Oscar Sherer State Park ("Sar8"), and Casperson Beach County Park and Brohard Park ("Sar7"). Other protected areas are very small: Lemon Bay Scrub County Park ("Sar4"), Myakka State Forest ("Sar14"), Charlotte Harbor State Buffer Preserve ("Char1").

Restoration potential: Habitat acquistion and restoration at Oscar Sherer State Park has increased the jay population from an estimated 19 pairs in 1992-1993, to 27 pairs in 1997, and when fully restored might support about 30 pairs (J. Thaxton, pers. comm.). The Casperson Beach County Park and Brohard park complex was estimated to support about 13 pairs of jays, compared to the 7 pairs found for the SMP.

Simulation results: This metapopulation ranked 16th in vulnerability (table 5-23), 8th in percent protected (56.2%; table 5-24), and 13th in priority (table 5-25), with moderate vulnerability and moderate potential for improvement.

The “no acquisition” option is estimated to support about 50 jay families after restoration and full occupancy. Simulation of this configuration indicated that the metapopulation is vulnerable to extinction (p=0.03) and quasi-extinction (0.10). Intermediate simulations (30% and 70%) did not produce any extinctions, and 2 simulations produced quasi-extinctions (Table 5-5b). Percent population declines were fairly large for all simulations, reflecting the large number of jays residing in small, somewhat isolated patches.

Recommendations: The relatively favorable ranking of this metapopulation is due mainly to the Oscar Sherer State Park population, which is much larger than any other local population and has a stable population trajectory. Considering that Oscar Sherer makes up a large proportion of the total metapopulation, the 40 to 50 percent population decline seen in the simulation results (Table 5-5b) is due to the collapse of the numerous smaller, somewhat isolated populations.

Acquisition of larger patches that are near other patches probably will benefit this population most. The best opportunity for acquisition appears to be the habitat patches in Charlotte county (“Char2”), southwest of the Rotunda Circle. Nearby patches in Rotunda Circle (“Char3” and “Char4”) also should be investigated, as jays in this area could provide dispersers to the protected but very isolated jays at Charlotte Harbor State Buffer Preserve (“Char1”). The possibility of bolstering the small protected jay population at Lemon Bay Scrub county park (“Sar4”) by acquiring nearby properties at “Sar3” and “Sar5” should be investigated. The private reserve (“Sar9”) just north of Oscar Sherer would benefit from the acquisition of “Sar10”.

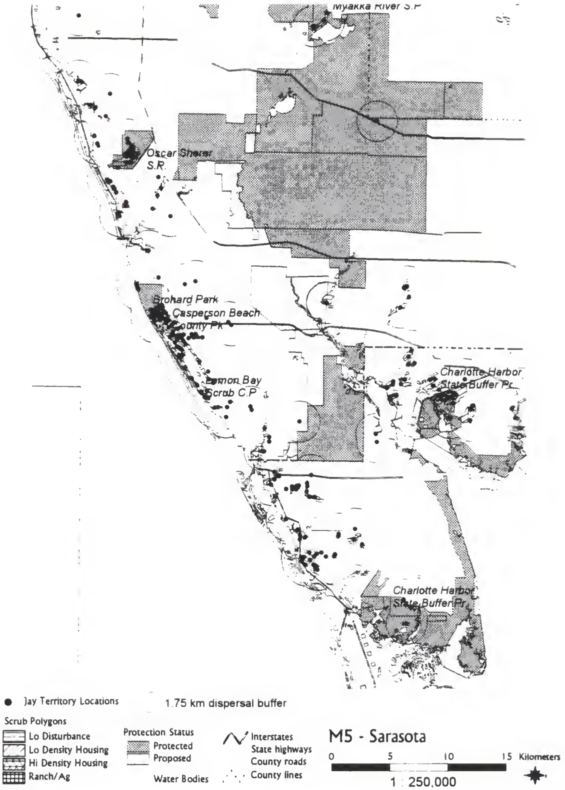


Fig. 5-5a. Sarasota and W. Charlotte county map – 1992 - 1993 jay and habitat distribution.

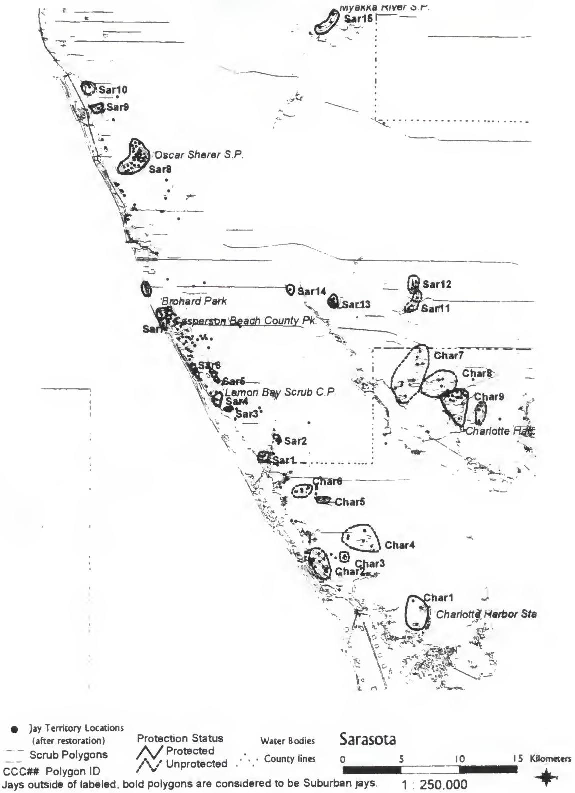
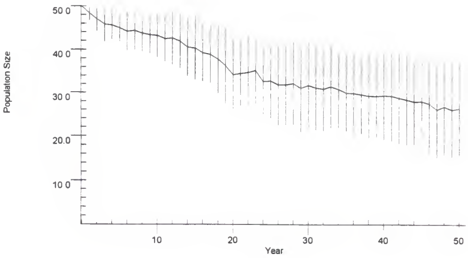


Fig. 5-5b. Sarasota and W. Charlotte county acquisition map.

Table 5-5a. Sarasota and W. Charlotte county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	30% preserved by contiguity	30% preserved by connectivity	70% preserved by contiguity	70% preserved by connectivity	Maximum acquisition
Char1	Charlotte Harbor S.B.P.	3	3	3	3	3	3	3
Char2		13		9	1	13	7	13
Char3		2			2	2	2	2
Char4		5			1	5	3	5
Char5		2					2	2
Char6		4			1		3	4
Sar1					1		1	2
Sar2		1			1		1	1
Sar3		1		1	1	1	1	1
Sar4	Lemon Bay Scrub Cty. Pk.	2	2	2	2	2	2	2
Sar5		1		1	1	3	2	3
Sar6		1			1		3	3
Sar7	Casperson Beach Cty. Pk./Brohard Pk.	7	13	13	13	13	13	13
Sar8	Oscar Sherer S.P.	19	30	30	30	30	30	30
Sar9	Private reserve	1	1	1	1	1	1	1
Sar10		2			1	3	2	3
Sar14	Myakka S.F.		1		1	1	1	1
Totals		64	50	61	61	77	77	89



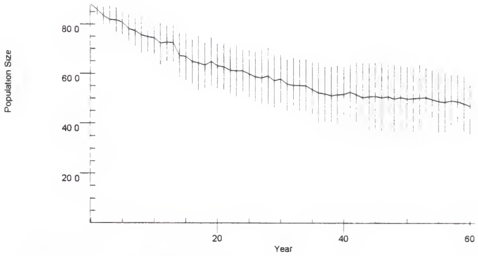
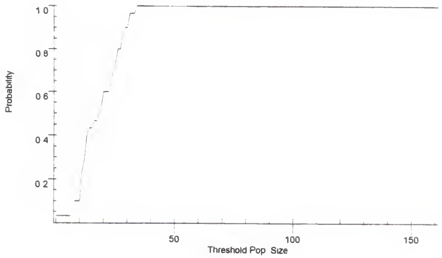


Fig. 5-5c. Sarasota and W. Charlotte county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



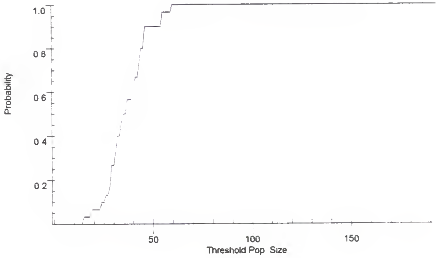


Fig. 5-5d. Sarasota and W. Charlotte quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-5b. Sarasota and W. Charlotte county simulation statistics

Data type	No acquisition	30% acquisition by connectivity	30% acquisition by area	70% acquisition by connectivity	70% acquisition by area	Maximum acquisition
starting population size	50	61	61	77	77	89
x end pop. size ± s.d.	26.3 10.7	31.3 9.6	33.6 8.0	43.9 11.1	45.7 13.2	46.9 11.6
percent decline	47.4	48.7	44.9	43.0	40.7	47.3
extinction risk	0.03	0.0	0.0	0.0	0.0	0.0
quasi-extinction risk (10 pairs)	0.10	0.07	0.0	0.0	0.02	0.0

N. W. Charlotte (M6)

General description: The N.W. Charlotte metapopulation is isolated from the Sarasota metapopulation to the west by the Myakka River, and is isolated from the Central Charlotte metapopulation to the east by the Peace River. The SMP documented about 44 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 28 pairs in currently protected areas, and 56 pairs maximum.

Protected areas: Protected jays occur on the Charlotte Harbor State Buffer Preserve ("Char9"; formerly known as Tippecanoe Scrub), and on the Myakka River State Forest ("Sar13"), a private reserve ("Char12") and near I-75 ("Char11a").

Restoration potential: Most patches in this metapopulation are small, and jay densities measured during the SMP were probably close to maximal. The Myakka River State Forest ("Sar13"), which had one pair of jays during the SMP, may have sufficient habitat for 6 pairs.

Simulation results: This metapopulation ranked 10th in vulnerability (table 5-23), 9th in percent protected (50.0%; table 5-24), and 6th in priority (table 5-25), with high vulnerability and high potential for improvement. All simulations had significant extinction and quasi-extinction risk, and large percent population declines (see Table 5-6b).

Recommendations: The risk estimates for the "maximum acquisition" configuration are greatly improved compared to the "no acquisition" option. Acquisition and restoration of as much habitat as possible is recommended. The most important population of protected jays in this metapopulation probably occurs at the Charlotte

Harbor State Buffer Preserve ("Char9"). Acquisition of unprotected habitat adjacent to this population ("Char8", Char7") should be a high priority. Additional habitat adjacent to the protected jays at Myakka State Forest ("Sar13") should be investigated for acquisition.

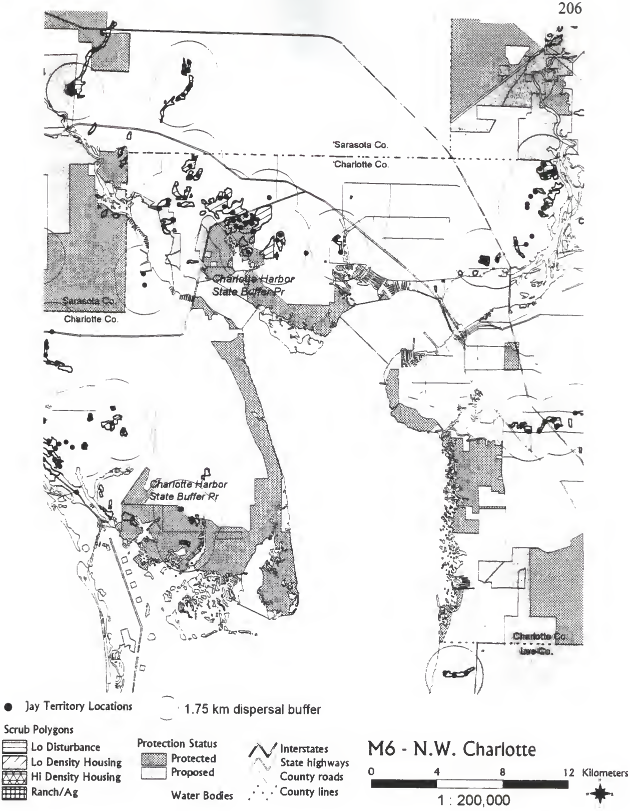


Fig. 5-6a. N. W. Charlotte county map – 1992 - 1993 jay and habitat distribution.

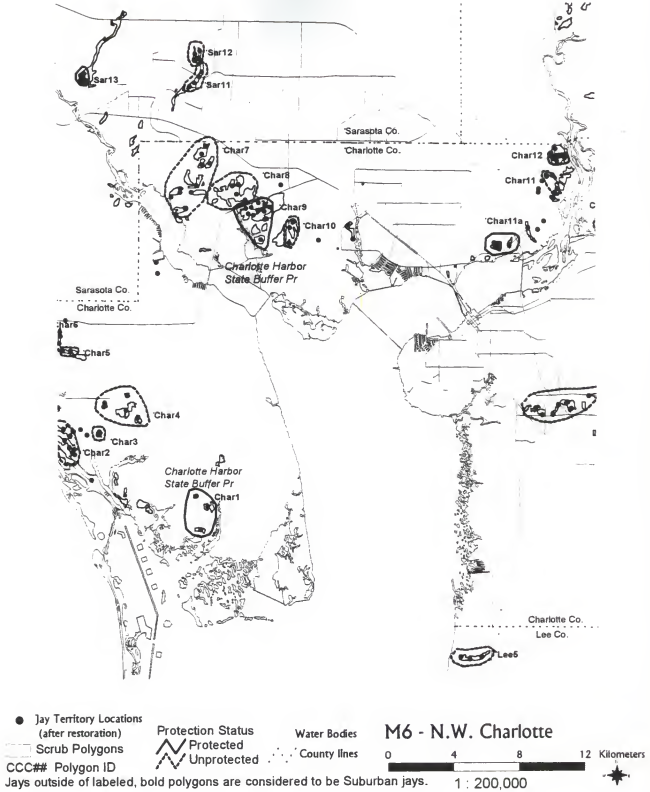
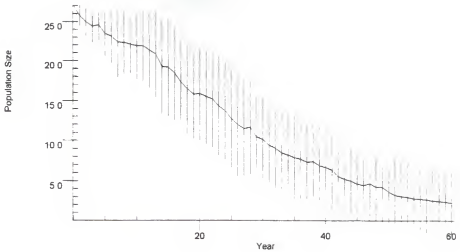


Fig. 5-6b. N. W. Charlotte county acquisition map.

Table 5-6a. N. W. Charlotte county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	70% preserved by connectivity	70% preserved by area	Maximum acquisition
Char7		11		8	11	11
Char8		4		3	4	4
Char9	Charlotte Harbor State Buffer Pr.	11	11	11	11	11
Char10		3		2	1	3
Char11		2		2	3	3
Char11a	SWFMD?	2	5	5	5	5
Char12	Private Pr.	6	6	6	6	6
Sar11		2		2		4
Sar12		2		2		4
Sar13	Myakka S.F.	1	6	6	6	6
Totals		44	28	47	47	56



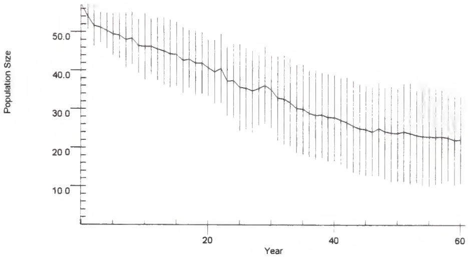
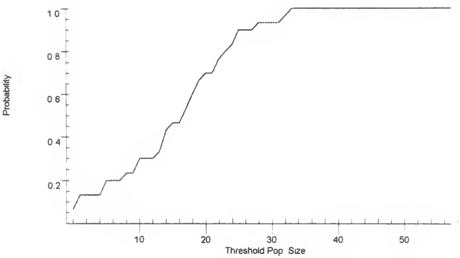


Fig. 5-6c. N. W. Charlotte county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



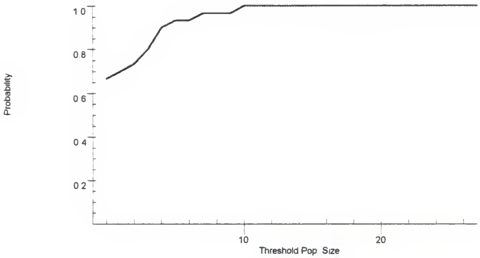


Fig. 5-6d. N. W. Charlotte county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-6b. N. W. Charlotte county simulation statistics

Data type	1992-1993 configuration	No acquisition	70% acquisition by connectivity	70% acquisition by area	Maximum acquisition
Starting population size	44	28	47	47	56
Mean ending population size ± s.d.	19.4 11.3	2.3 3.9	12.8 9.1	14.5 8.6	22.1 11.3
% population decline	55.9	91.8	72.8	69.1	60.7
Extinction Risk	0.10	0.67	0.17	0.17	0.07
Quasi-extinction Risk (10 pairs)	0.37	1.0	0.63	0.57	0.30

Central Charlotte (M7)

General description: The central Charlotte metapopulation is isolated from the nearby northwest Charlotte metapopulation by the Peace River to the west. Most of the habitat occurs along Prairie and Shell Creek, which drain into the Peace River. Two somewhat isolated populations occur south of Punta Gorda ("Char22") and into Lee county ("Lee5"), the latter patch occurring near a proposed Carl addition to the Babcock-Webb W.M.A. The SMP documented about 31 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 5 pairs in currently protected areas, and 61 pairs maximum.

Protected areas: No jays are protected on public lands in this metapopulation; a small population of jays occurs on a private reserve ("Char16").

Restoration potential: The restoration potential for most patches in this metapopulation probably is not significantly greater than the jay densities measured for the SMP. However, two large incompletely surveyed patches occur along Prairie Creek ("Char17", "Char18") and may have large restoration potential. For modeling purposes, these patches were estimated to support considerably more jays than were found during the SMP (Table 5-7a). Both patches probably have the potential to support substantially more jays than the estimates used here. A large, unsurveyed patch east of "Char20" along Shell Creek may harbor jays, but no jays were included in any of the simulations.

Simulation results: This metapopulation ranked 2nd in vulnerability (table 5-23), 19th in percent protected (8.2%; table 5-24), and 3rd in priority (table 5-25), with high vulnerability and high potential for improvement. The "no acquisition" option is

extremely vulnerable to extinction and quasi-extinction (Table 5-7b). The "70% acquisition by area" configuration is considerably improved, but still has a substantial quasi-extinction risk (p=0.33). The "maximum acquisition" has a much lower quasi-extinction risk (p=0.07).

Recommendations: This metapopulation ranks 2nd in vulnerability due to the near absence of jays on protected lands. It has a priority ranking of 3, with low protection and high potential for improvement.

The private reserve ("Char16") would benefit considerably by the acquisition of nearby jay habitat, especially "Char15". Substantial tracts of largely unsurveyed, unprotected scrub occur along both sides of Prairie Creek ("Char17", "Char18"), and jays were documented in the western portions of these patches for the SMP. Acquisition and restoration of these patches would greatly bolster this metapopulation. The large, unsurveyed patch along Shell Creek also should be investigated. Consideration should be given to adding the isolated scrub patch ("Lee 5") to the proposed CARL addition to the Babcock-Webb W.M.A.

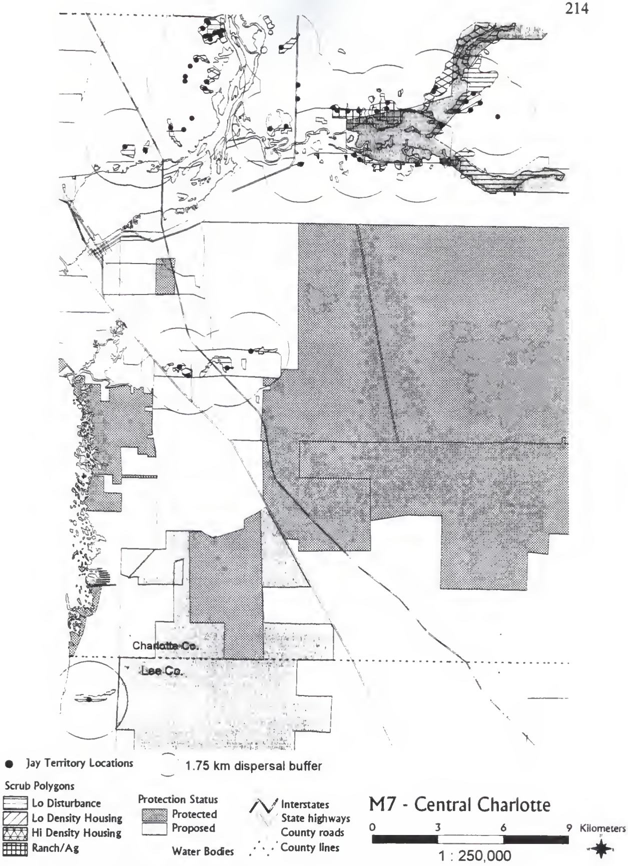


Fig. 5-7a. Central Charlotte county map – 1992 – 1993 jay and habitat distribution..

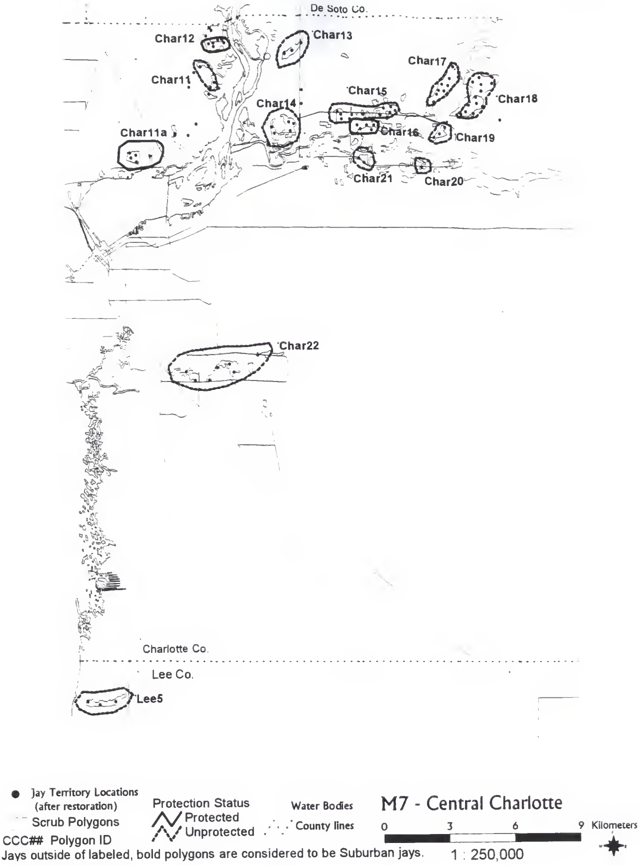
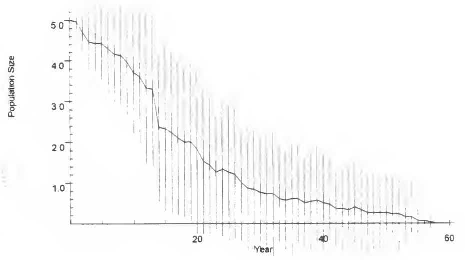


Fig. 5-7b. Central Charlotte county acquisition map.

Table 5-7a. Central Charlotte county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	30% acquisition by connectivity	30% acquisition by area	70% acquisition by connectivity	70% acquisition by area	Maximum acquisition
Char13		1		1		2		3
Char14		2		2		3	5	5
Char15		7		2	11	7	11	11
Char16	private reserve	5	5	5	5	5	5	5
Char17		2		3	6	6	9	9
Char18		5		4		9	12	12
Char19		1		1		2		3
Char20		1		1		1		1
Char21		2		1		2	2	2
Char22		4		2		5		7
Lee5		1		1		2		3
Totals		31	5	22	22	44	44	61



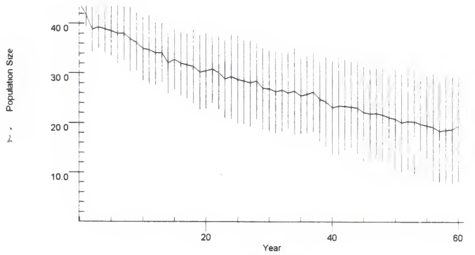
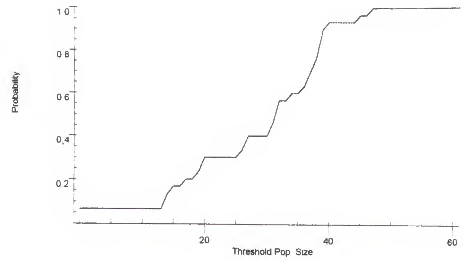


Fig. 5-7c. Central Charlotte county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



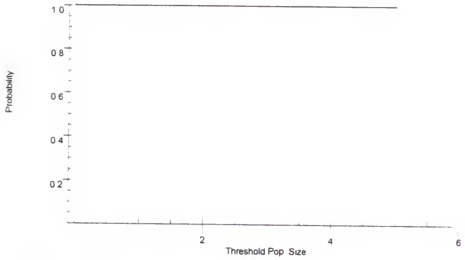


Fig. 5-7d. Central Charlotte county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-7b. Central Charlotte county simulation statistics

Data type	Original 1992-1993 scenario	No acquisition	70% acquisition by connectivity	70% acquisition by area	Maximum acquisition
starting population size	31	5	44	44	61
x end pop. size ± s.d.	11.7 6.3	0.0 0.0	21.3 10.4	35.5 10.4	19.4 11.3
percent decline	62.2	100.0	51.6	19.3	65.4
extinction risk	0.13	1.0	0.17	0.10	0.07
quasi-extinction risk (10 pairs)	0.70	1.0	0.30	0.33	0.07

Lee and N. Collier (M8)

General description: The Lee metapopulation is isolated from the N.W. Charlotte metapopulation by the heavily forested Babcock-Cecil Webb Wildlife Management Area. The Lee metapopulation is just beyond the 12km dispersal buffer of the Lake Wales Ridge metapopulation, but the intervening habitat may be conducive to some exchange between these metapopulations. Jays within the Lee metapopulation are poorly connected; jays occur in tiny patches along the Caloosahatchee River, a second cluster occurs around the town of Immokalee, and a few jays occur near the Gulf Coast at Estero Bay and into Collier county. A small experimental population of jays has been translocated to Rookery Bay south of Naples (Mumme and Below 1999). The SMP documented about 47 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 15 pairs in currently protected areas, and 62 pairs maximum.

Protected areas: Protected jays occur on Estero Bay Aquatic Preserve ("Lee3"), and at Rookery Bay National Estuarine Research Reserve ("Coll2").

Restoration potential: Restoration potential of this metapopulation is quite limited for jays except near the Gulf Coast. Estero Bay Aquatic Preserve ("Lee3") might support about 9 pairs of jays after restoration, and the unprotected habitat 7-8 km south at "Coll1" might support about 7 pairs. Some large habitat patches between "Lee3" and "Coll1" appear to be unoccupied because of heavy overgrowth.

Simulation results: This metapopulation ranked 9th in vulnerability (table 5-23), 16th in percent protected (24.2%; table 5-24), and 9th in priority (table 5-25), with high vulnerability and moderate potential for improvement. The "no acquisition" option has a

high risk of extinction (p=0.73) and quasi-extinction (p=1.0; Table 5-8b). The "maximum acquisition" option shows a moderate risk of extinction (p=0.40) and a high risk of quasi-extinction (p=0.90).

Recommendations: The best opportunities for acquisition and restoration appear to be at the Estero Bay Aquatic Preserve ("Lee3") and south to "Coll1", including the intervening unoccupied patches. Management of jay habitat at the Immokalee airport ("Coll3") and acquisition of nearby patches should be investigated. The acquisition of unprotected jay habitat near the Caloosahatchee State Recreation Area ("Lee2") and near the Hickey Creek Mitigation Park ("Lee1") also should be investigated. Mumme and Below (1999) state that more intensive habitat management is needed for the experimental translocation at Rookery Bay to succeed.

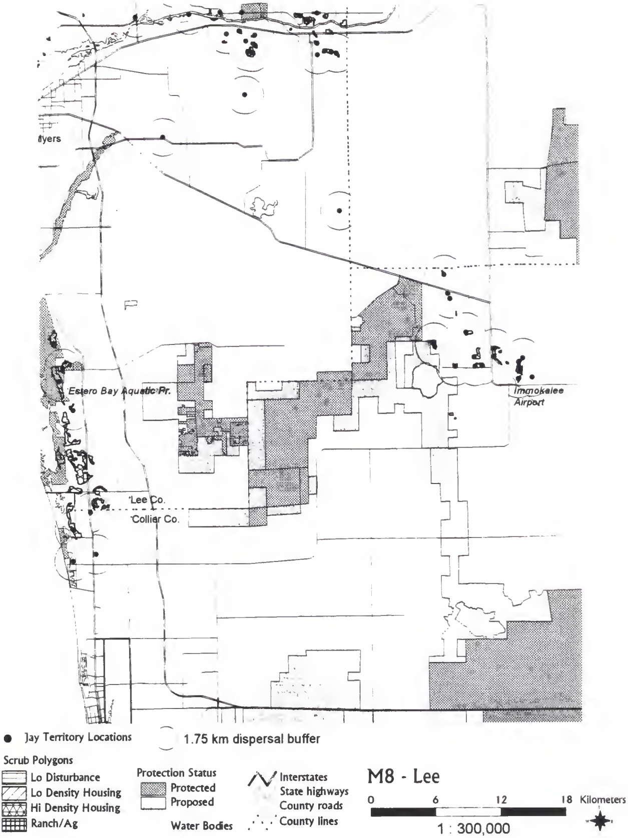


Fig. 5-8a. Lee and N. Collier county map – 1992 - 1993 jay and habitat distribution.

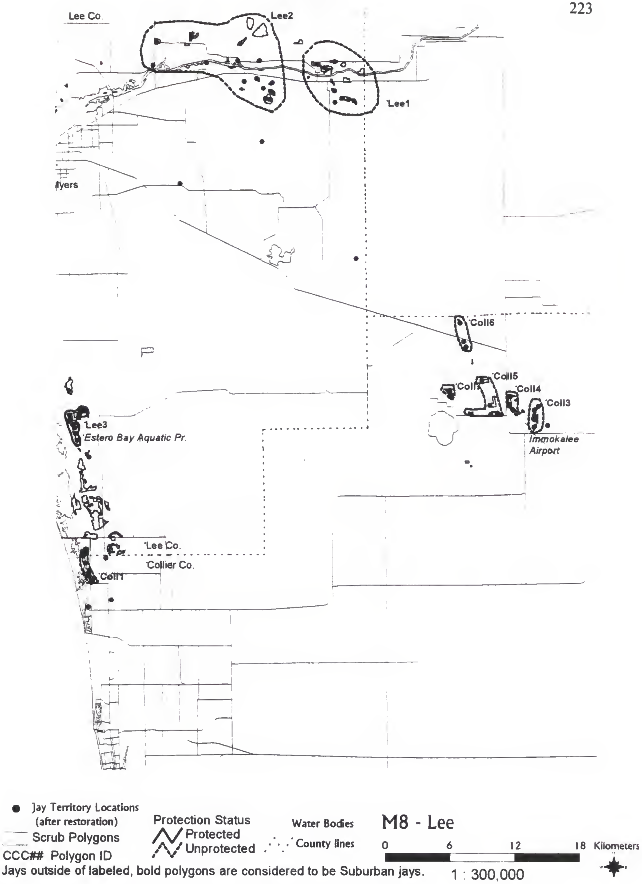
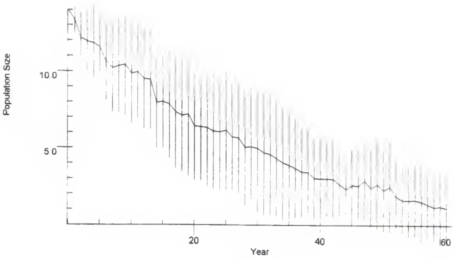


Fig. 5-8b. Lee and N. Collier county acquisition map.

Table 5-8a. Lee and N. Collier county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	30% acquisition by area	70% acquisition by area	Maximum acquisition
Lee1		8			6	8
Lee2		15			8	15
Lee3	Estero Bay Aquatic Pr.	2	9	9	9	9
Lee4		1				1
Coll1		2		6	6	7
Coll2	Rookery Bay Nat. Estuarine Research Reserve	3	6	6	6	6
Coll3	Immokalee Airport	4		4	4	4
Coll4		2			2	2
Coll5		5			5	5
Coll6		3				3
Coll7		2			2	2
Totals		47	15	25	48	62



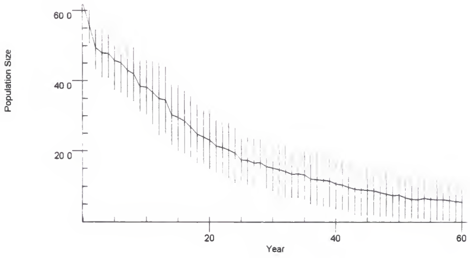
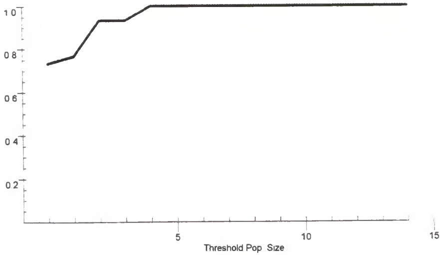


Fig. 5-8c. Lee and N. Collier county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



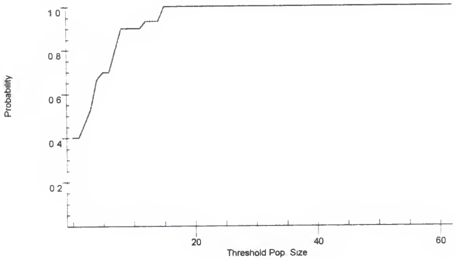


Fig. 5-8d. Lee and N. Collier county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-8b. Lee and N. Collier county simulation statistics

Data type	Original 1992-1993 scenario	No acquisition	30% acquisition by area	70% acquisition by area	Maximum acquisition
starting population size	47	15	25	48	62
x end pop. size ± s.d.	0.9 2.4	1.1 2.2	2.0 3.2	4.5 6.1	5.6 4.7
percent decline	98.0	92.7	92.0	90.1	91.0
extinction risk	0.87	0.73	0.67	0.43	0.40
quasi-extinction risk (10 pairs)	1.0	1.0	1.0	0.90	0.90

Flagler-N.E. Volusia (M9)

General description: The Flagler-N.E. Volusia county metapopulation is the most north-eastern population of jays occurring along the Atlantic Coast. This metapopulation is isolated from the Volusia-Merritt Island metapopulation (m10) to the south by the city of Daytona Beach. All of the jays in this metapopulation occur near or along the beach; consequently habitat loss due to oceanfront development has greatly reduced this population. The SMP documented about 12 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 5 pairs in currently protected areas, and 12 pairs maximum.

Protected areas: The only protected jays in this metapopulation occur in the N. Peninsula State Recreation Area ("Vol1" in Fig. 5-9b). Three protected areas had jays prior to the SMP: Gamble Rogers Memorial State Recreation Area, Flagler Beach State Recreation Area, and Washington Oaks State Gardens (jays still occasionally seen). Jays occur near these parks, as well as near Marineland, but appear to occupy territories in suburban or urban settings.

Restoration potential: Improved management of the unoccupied, protected areas (Gamble Rogers, Flagler Beach, and Washington Oaks) might attract jays from nearby suburban settings. The potential also exists to re-introduce jays to these parks, but for modeling purposes jays were excluded from these areas. The population of jays at N. Peninsula State Recreation Area as measured for the SMP was assumed to be close to carrying capacity.

Simulation results: This metapopulation ranked 7th in vulnerability (table 5-23), 10th in percent protected (41.7%; table 5-24), and 16th in priority (table 5-25), with high

vulnerability and low potential for improvement. Simulations of the currently protected configuration of 5 territories produced a high extinction (p=0.933) and quasi-extinction risk (p=1.0) for the small population (Table 5-9b). The "maximum acquisition" option produced a substantially reduced extinction risk (p=0.57; Table 5-9b), but the quasi-extinction risk remained high (p=1.0).

Recommendations: The habitat map for this metapopulation developed for the SMP is based on old soil maps and is very outdated along the coast; it does not reflect the extensive habitat destruction that has occurred subsequent to the production of the soil maps. Recent aerial photographs should be used to update this habitat information.

Acquisition options are very limited along the coast in this area. The best opportunity may be several small tracts of land near Marineland and Washington Oaks ("Flag1", "Flag2"). The prognosis for this small population of jays is not good, as they probably face problems similar to those described by Breininger (1999) for the urban jays on the the south Brevard county barrier island. Some large tracts of apparently unoccupied scrub may still exist a few kilometers inland. Given the high risk faced by the coastal jays and their potentially unique genetic traits, the possibility of acquiring and restoring these unoccupied patches and translocating jays from nearby coastal areas should be considered.

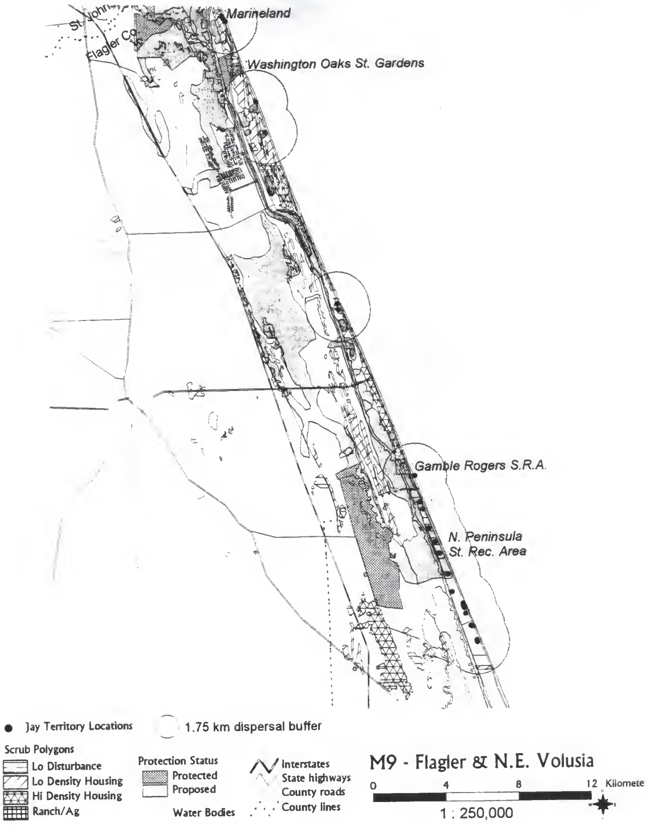


Fig. 5-9a. Flagler and N.E. Volusia county map – 1992 – 1993 jay and habitat distribution.

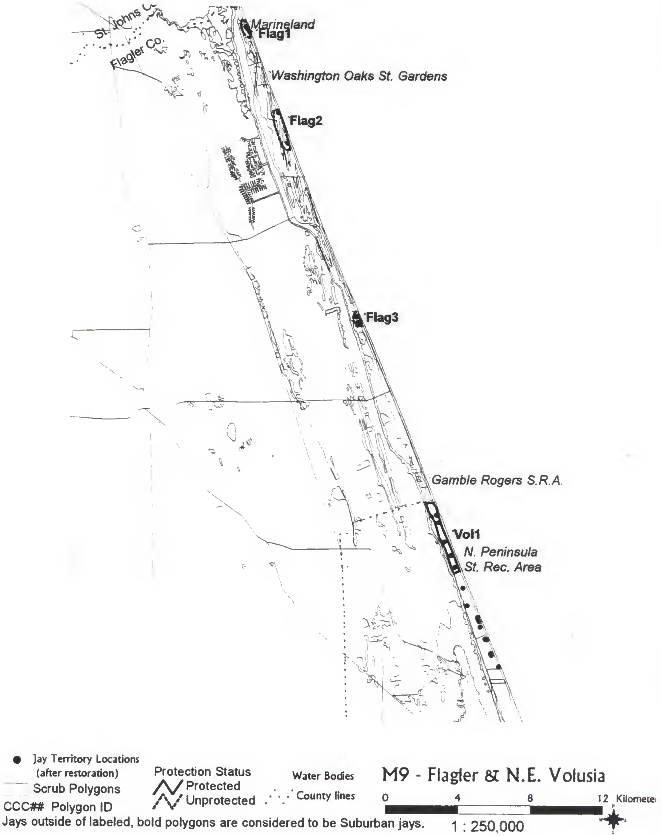
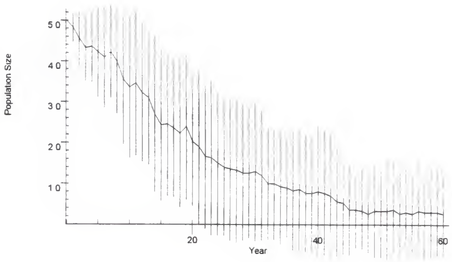


Fig. 5-9b. Flagler and N.E. Volusia county acquisition map.

Table 5-9a. Flagler and N.E. Volusia county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	Maximum acquisition
Flag1		3		3
Flag2		2		2
Flag3		2		2
Vol1	N. Peninsula St. Rec. Area	5	5	5
Totals		12	5	12



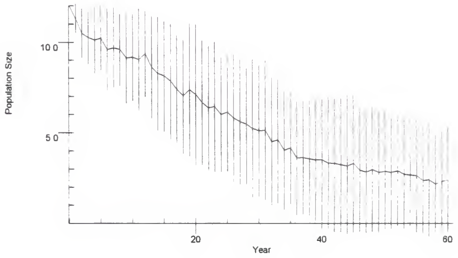
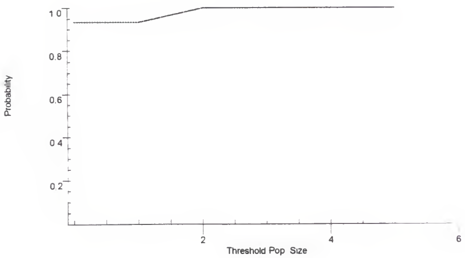


Fig. 5-9c. Flagler and N.E. Volusia county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



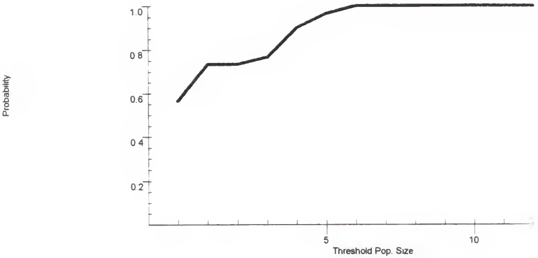


Fig. 5-9d. Flagler and N.E. Volusia county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-9b. Flagler and N.E. Volusia county simulation statistics

Data type	Original 1992-1993 scenario	No acquisition	Maximum acquisition
Starting population size	12	5	12
Mean ending population size ± s.d.	2.4 2.91	0.27 0.995	2.4 2.91
Percent population decline	75.8	80.1	75.8
Extinction Risk	0.57	0.933	0.57
Quasi-extinction Risk (10 pairs)	1.00	1.00	1.00

Merritt Island-S.E. Volusia and (M10)

General description: This metapopulation includes a large number of protected jays on the huge barrier island complex that includes Cape Canaveral Air Station (CCAS), Kennedy Space Center (KSC), and Merritt Island National Wildlife Refuge (MINWR). A few unprotected jays occur just north of MINWR in Volusia county, and along the eastern and southern boundaries of MINWR and south of CCAS. This metapopulation is isolated from the Flagler-N.E. Volusia metapopulation by the city of Daytona Beach to the north, and from the N. Brevard metapopulation by the Indian River and Turnbull Hammock to the west and southwest. The SMP documented about 536 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 495 pairs in currently protected areas, and 536 pairs maximum.

Protected areas: Protected jays occur within CCAS, KSC, MINWR, and several small reserves (Table 5-10a).

Restoration potential: The restoration potential of KSC and MINWR is difficult to estimate due to the heterogeneous nature of the habitat. The habitat information provided by the SMP is much too coarse to attempt an assessment. Because the population sizes estimated for the SMP are quite large, the simulation results would not be affected significantly by increasing the population size above the SMP estimates. Consequently, densities estimated by the SMP were used for all simulations.

Simulation results: This metapopulation ranked 19th in vulnerability (table 5-23), 2nd in percent protected (92.3%; table 5-24), and 19th in priority (table 5-25), with low vulnerability and low potential for improvement.The "no acquisition" configuration and

"maximum acquisition" option produced very similar results, with no extinction or quasi-extinction risk and very low percent population declines (Table 5-10b).

Recommendations: Although this is a large metapopulation, vulnerability to hurricanes, habitat overgrowth and difficulties with habitat restoration pose serious threats to this metapopulation. Modeling performed by Breininger et al. (in press) found this metapopulation to be vulnerable to catastrophes associated with hurricanes, but habitat degradation was a much more important risk factor. Years of fire suppression have resulted in overgrown habitat which is difficult to restore compared to other areas, apparently because the coastal soils and water table allow rapid regrowth of scrub oaks and other vegetation, resulting in the closure of openings needed by jays for foraging and predator detection. Preliminary results from a 1999 survey of MINWR/KSC suggest that the population may have declined as much as 50% compared to estimates made during the SMP (Gary Popotnik, pers. comm.). Habitat restoration is urgently needed for this metapopulation.

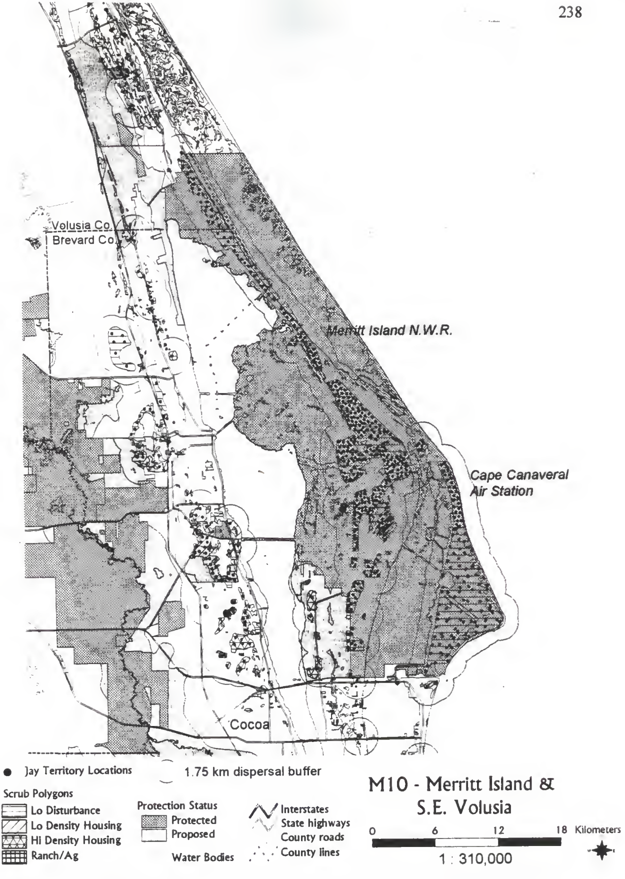


Fig. 5-10a. Merritt Island and S.E. Volusia county map – 1992 - 1993 jay and habitat distribution.

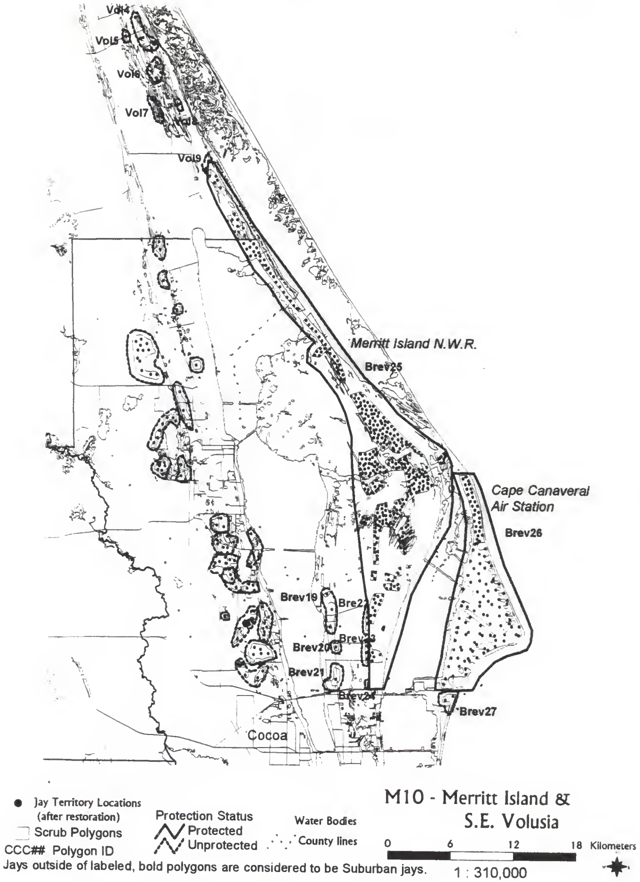
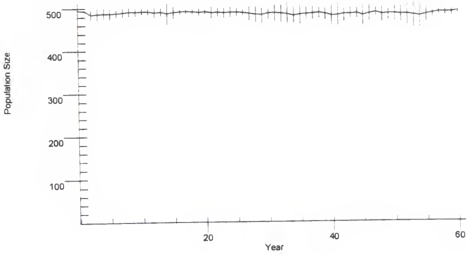


Fig. 5-10b. Merritt Island and S.E. Volusia county acquisition map.

Table 5-10a. S.E. Volusia and Merritt Island county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	Maximum acquisition
Vol2		3		3
Vol3		4		4
Vol4		7		7
Vol5		1		1
Vol6		6		6
Vol7		4		4
Vol8		1		1
Vol9		2		2
Brev19		4		4
Brev20		3		3
Brev21		3		3
Brev22		1		1
Brev23		1		1
Brev24		1		1
Brev25	Merritt Island N.W.R. & Kennedy Space Center	377	377	377
Brev26	Cape Canaveral Air Station	118	118	118
Totals		536	495	536



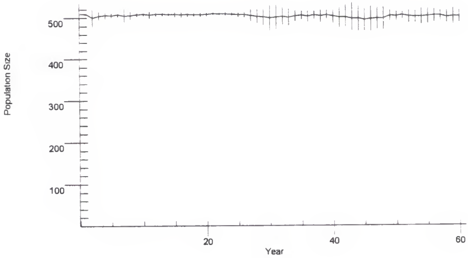
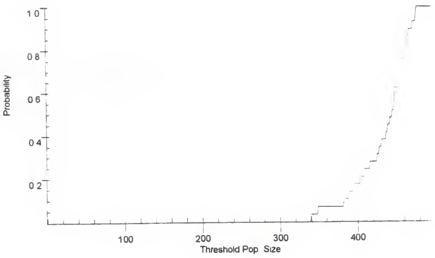


Fig. 5-10c. S.E. Volusia and Merritt Island county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



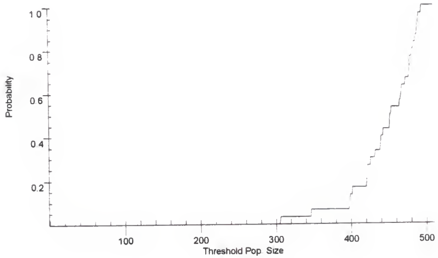


Fig. 5-10d. S.E. Volusia and Merritt Island county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-10b. S.E. Volusia and Merritt Island county simulation statistics

Data type	No acquisition	Maximum acquisition
starting population size	495	536
x end pop. size ± s.d.	491.5 5.7	501.3 14.5
percent decline	0.7	6.5
extinction risk	0.0	0.0
quasi-extinction risk (10 pairs)	0.0	0.0

N. Brevard (M11)

General description: The N. Brevard metapopulation is separated from the Central Brevard metapopulation (M12) by the city of Cocoa, and from the S.E. Volusia and Merritt Island metapopulation by the Indian River and Turnbull Hummock to the east and northeast (see Fig. 5-11a). The SMP documented about 101 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 4 pairs in currently protected areas, and 110 pairs maximum.

Protected areas: Few or no jays occur on protected lands in N. Brevard. For modeling purposes, protected jays were assumed to occur only on recently acquired property at South Lake ("Brev7"). Several properties that are targeted for acquisition include Seminole Ranch ("Brev8"), Buck Lake ("Brev4"), and Tico ("Brev12", "Brev11", and "Brev10"; see Fig. 5-11b). The Dicerandra Scrub Sanctuary falls within "Brev10", and the Enchanted Forest Sanctuary falls within "Brev11", but apparently neither property has scrub-jays.

Restoration potential: At the time of the SMP, jay densities in most areas were probably close to maximum (compare first and last data columns in Table 5-11a). Restored population sizes were increased slightly for Buck Lake ("Brev4") and Seminole Ranch ("Brev8").

Simulation results: This metapopulation ranked 3rd in vulnerability (table 5-23), 20th in percent protected (3.6%; table 5-24), and 1st in priority (table 5-25), with high vulnerability and high potential for improvement.

The small number of jays currently protected are extremely vulnerable to extinction (p=1.0) and quasi-extinction (p=1.0; Table 5-11a). The 30% acquisition configuration, weighted by area, was estimated to support about 33 jay families concentrated in only 4 patches currently protected or targeted for acquisition (Table 5-11a). Simulations of this configuration indicated that the population is vulnerable to quasi-extinction (Table 5-11b and Fig. 5-11a; quasi-extinction = 0.40). The mean population trajectory showed a 48.8% decline (Fig. 5-11b). The 30% acquisition configuration, weighted by connectivity, was considerably worse than the area-weighted configuration (Table 5-11b).

Simulations of the 70% acquisition configurations indicate that the population would not be vulnerable to extinction and or quasi-extinction risk (Table 5-11b). The mean percent population decline was considerably better for the area-weighted configuration (20.8%) than the connectivity-weighted configuration 38.7%Table 5-11b).

The maximum acquisition configuration was estimated to support about 110 jay families (Table 5-11a). Simulations of this configuration indicate that the population would not be vulnerable to extinction or quasi-extinction, and had a low mean percent population decline (16.7%; Table 5-11b).

Recommendations: This high priority (#1) metapopulation is second-to-last in percent protected jays, and needs substantial acquisition to adequately protect its remaining jays. The acquisition and restoration of proposed properties listed for the 30% area configuration (Table 5-11a: Buck Lake, South Lake, Seminole Ranch, and portions of Tico) is insufficient to secure this metapopulation (quasi-extinction risk = 0.40). The viability of this metapopulation would be greatly increased by expanding the proposed

properties (especially around Tico and Seminole Ranch), and the acquisition and restoration of some of the southern habitat patches (“Brev15”, “Brev16”, “Brev17”, “Brev18”).

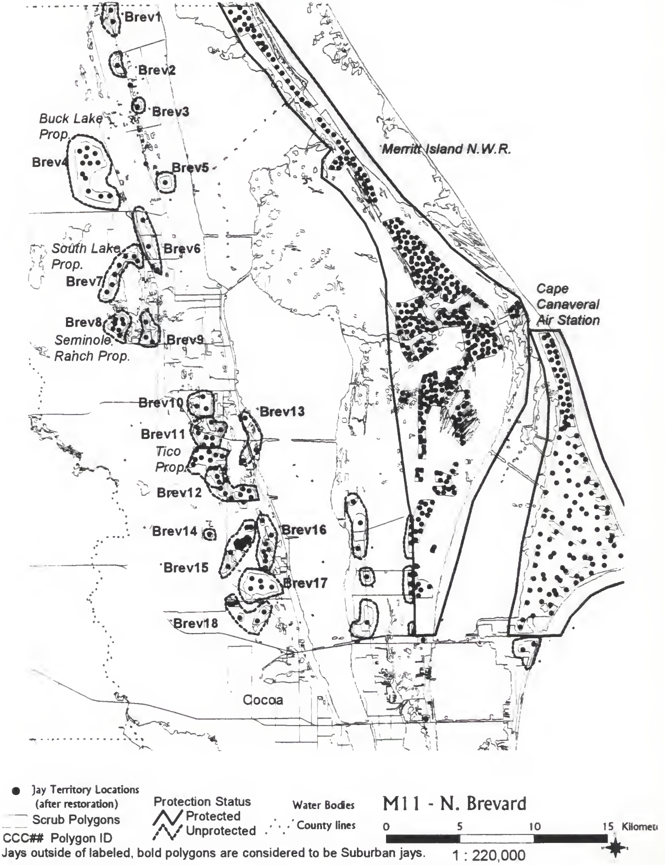


Fig. 5-11a. N. Brevard county map – 1992 - 1993 jay and habitat distribution.

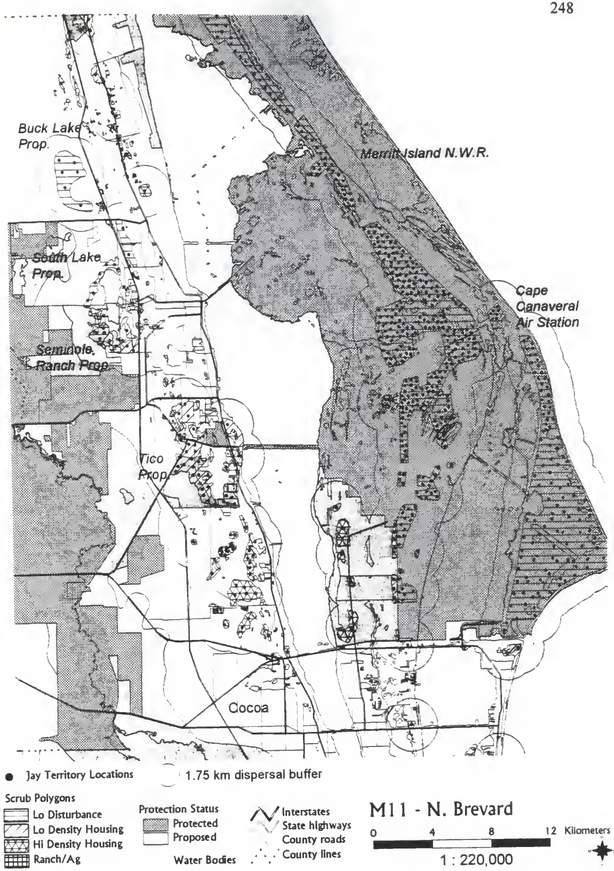
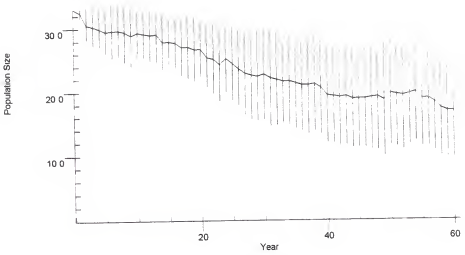


Fig. 5-11b. N. Brevard county acquisition map.

Table 5-11a. N. Brevard county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	30% preserved by contiguity	30% preserved by connectivity	70% preserved by contiguity	70% preserved by connectivity	Maximum acquisition
Brev1		2			1		1	2
Brev2		1			1		1	1
Brev3		1			1		1	1
Brev4	(Buck Lake - proposed)	6		13	6	13	13	13
Brev5		1						1
Brev6		4			2		2	4
Brev7	South Lake (partial)	7	4	7	4	7	7	7
Brev8	(Seminole Ranch - proposed)	5		7	2	7	7	7
Brev9		3			3		3	3
Brev10		3					3	3
Brev11		8				3	4	8
Brev12	(Tico – partial/ proposed))	21		6	4	21	12	21
Brev13		3					3	3
Brev14		1						1
Brev15		16			3	14	9	16
Brev16		8			2	7	4	8
Brev17		5			1	5	3	5
Brev18		6						6
Totals		101	4	33	33	77	77	110



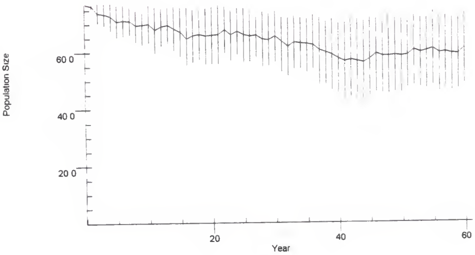
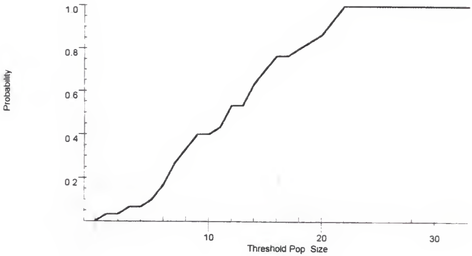


Fig. 5-11c. N. Brevard county trajectory graphs. Top) 30% acquisition, Bottom) 70% acquisition.



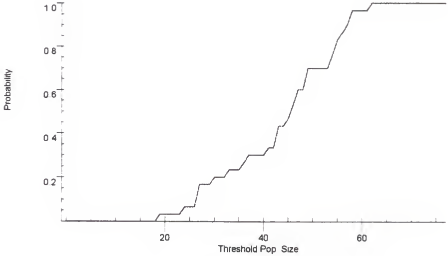


Fig. 5-11d. N. Brevard county quasi-extinction graphs. Top) 30% acquisition, Bottom) 70% acquisition.

Table 5-11b. N. Brevard county simulation statistics

Data type	No acquisition	30% acquisition by connectivity	30% acquisition by area	70% acquisition by connectivity	70% preserved by area	Maximum acquisition
starting population size	4	33	33	77	77	110
x end pop. size ± s.d.		5.5 4.6	16.9 7.4	47.2 19.2	61.0 12.6	91.5 11.4
percent decline		83.3	48.8	38.7	20.8	16.7
extinction risk		0.37	0.0	0.0	0.0	0.0
quasi-extinction risk (10 pairs)		0.90	0.40	0.0	0.0	0.0

Central Brevard (M12)

General description: The Central Brevard metapopulation is separated from the N. Brevard metapopulation (M11) by the city of Cocoa, from the S. Brevard- Indian River- N. St. Lucie metapopulation (M13) by the city of Melbourne, and from the Merritt Island metapopulation (M10) to the east by the Indian River (see maps in Fig. 5-12a, b). The SMP documented about 36 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 5 pairs in currently protected areas, and 40 pairs maximum.

Protected areas: Rockledge Scrub Preserve ("Brev40"); Wickham County Park ("Brev43). Portions of the large, contiguous habitat patch ("Brev41") just south of Rockledge are targeted for acquisition (1999 Carl project), as is habitat ("Brev42" – CARL 1999 site) just north of Wickham County Park. The Melbourne regional airport ("Brev29"), which lacks a habitat management plan, was not included as a protected area.

Restoration potential: At the time of the SMP, jay densities in most areas probably were close to maximum (compare first and last data columns in Table 5-12a).

Simulation results: This metapopulation ranked 4th in vulnerability (table 5-23), 18th in percent protected (12.5%; table 5-24), and 4th in priority (table 5-25), with high vulnerability and high potential for improvement. The "no acquisition" option has an extremely high probability of extinction (p=1.0) and quasi-extinction (p=1.0). The "70% acquisition by area" has a high quasi-extinction risk (p=0.43) and a moderate extinction risk (p=0.10). Risk estimates for the "maximum acquisition" option are substantially reduced for both quasi-extinction (p=0.0) and extinction (p=0.10), as is percent population decline (see Table 5-12b).

Recommendations: Although afforded little protection, the viability of this metapopulation could be greatly increased through acquisition of the few remaining habitat patches. The long term viability of this metapopulation and the small Rockledge Scrub Preserve ("Brev40") depends critically on substantial acquisition and restoration of habitat at "Brev41" (EELS/CARL 1999 site). The small population at Wickham County Park ("Brev43") would benefit greatly from proposed acquisition of habitat just to the north ("Brev42" – 1999 CARL). A habitat management plan is needed for the jays at Melbourne Regional Airport ("Brev44").

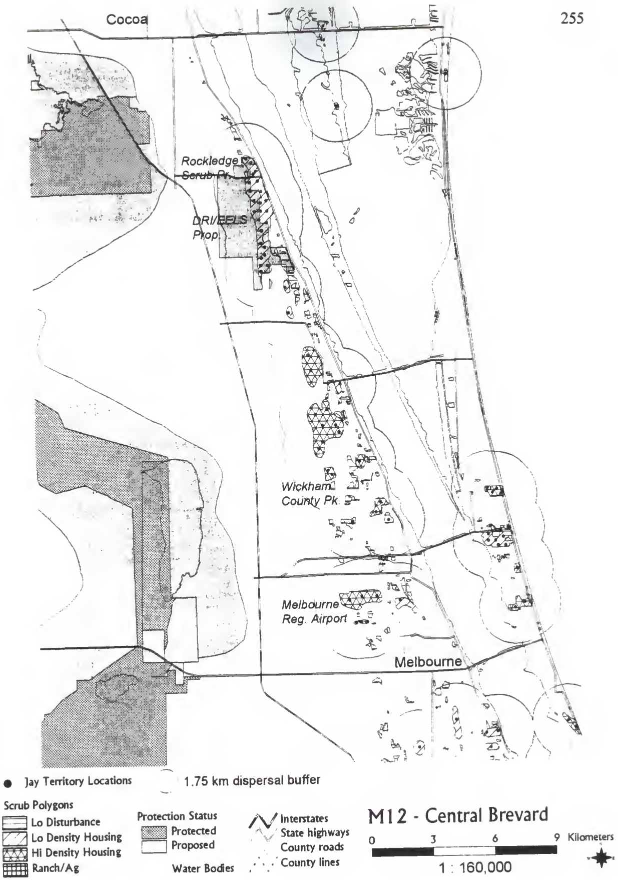


Fig. 5-12a. Central Brevard county map – 1992 – 1993 jay and habitat distribution.

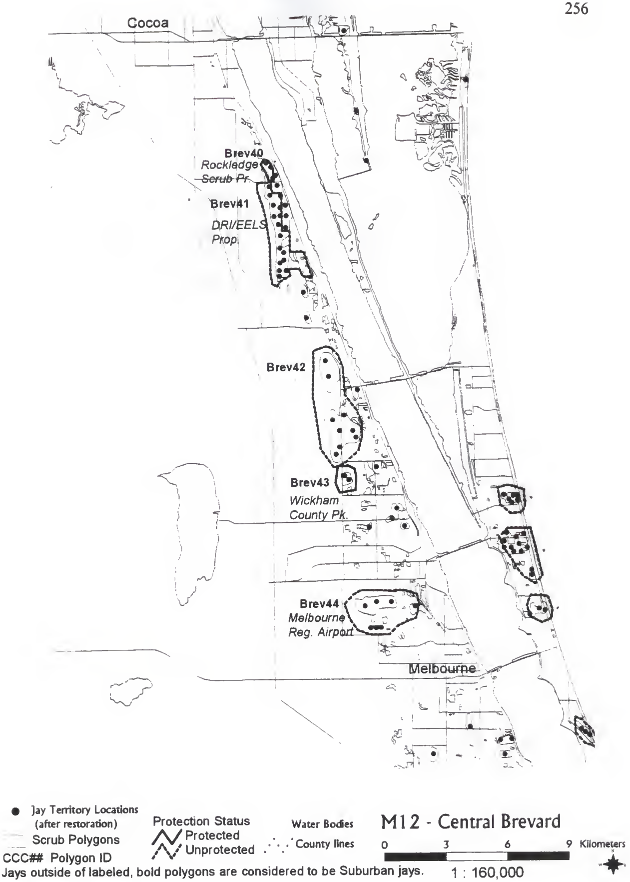
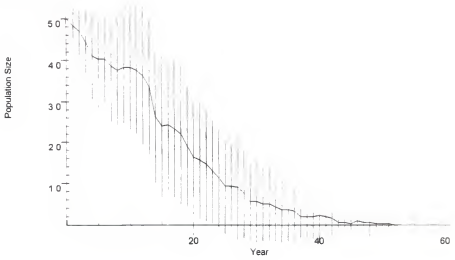


Fig. 5-12b. Central Brevard county acquisition map.

Table 5-12a. Central Brevard county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	70% preserved by area	Maximum acquisition
Brev40	Rockledge Scrub Pr.	3	3	3	3
Brev41	(DRI/EELS - proposed)	15		16	19
Brev42	(Wickham Rd. CARL site)	9		9	9
Brev43	Wickham County Pk.	2	2	2	2
Brev44	Melbourne regional airport	7			7
Totals		36	5	30	40



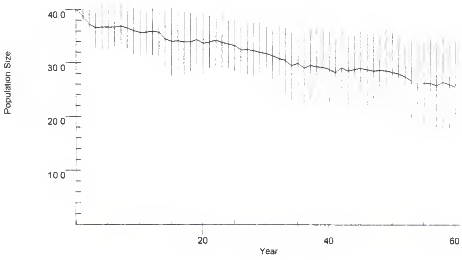
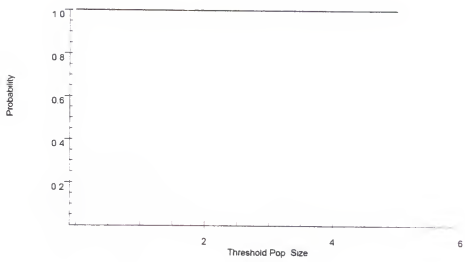


Fig. 5-12c. Central Brevard county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



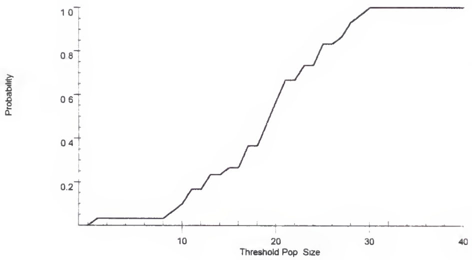


Fig. 5-12d. Central Brevard county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-12b. Central Brevard county simulation statistics

Data type	No acquisition	70% acquisition by area	Maximum acquisition
starting population size	5	30	40
x end pop. size ± s.d.	0 0.0	15.0 6.4	25.5 8.8
percent decline	100.0	50.0	36.3
extinction risk	1.0	0.10	0.00
quasi-extinction risk (10 pairs)	1.0	0.43	0.10

S. Brevard-Indian River-N. St. Lucie (M13)

General description: The S. Brevard-Indian River-N. St. Lucie metapopulation is separated from the Central Brevard metapopulation (M12) by the city of Melbourne, from the St. Lucie metapopulation (M14) to the south by Fort Pierce, and from the Merritt Island metapopulation (M10) to the east by the Indian River (see maps in Fig. 5-13a,b). The SMP documented about 153 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 62 pairs in currently protected areas, and 165 pairs maximum.

Protected areas: Malabar Scrub Preserve ("Brev30"), Valkaria Scrub Preserve ("Brev32/32a"), St. Sebastian River State Buffer Preserve ("Brev35"), private HCP ("InRi3"), Wabassa Scrub Preserve ("InRi3"). Since the SMP, an additional 12 territories were discovered in the N. Indian River county portion of the St. Sebastian River State Buffer Preserve (Dave Breininger, pers. comm.). Two jay populations on airports (Sebastian Municipal; St. Lucie County) were treated as unprotected due to lack of habitat management.

Restoration potential: The restoration potential for most patches in this metapopulation probably is not significantly greater than the jay densities measured for the SMP (compare first and last data columns in Table 5-13a).

Simulation results: This metapopulation ranked 15th in vulnerability (table 5-23), 13th in percent protected (37.6%; table 5-24), and 11th in priority (table 5-25), with moderate vulnerability and moderate potential for improvement. Simulations of the "no acquisition" configuration indicate that currently protected jays are vulnerable to quasi-

extinction (Table 5-13b and Fig. 5-13f; quasi-extinction risk = 0.167) and show a substantial population decline (Table 5-13b and Fig. 5-13e; mean ending population size = 32.5; percent decline = 50.0). Intermediate configurations all show a substantial reduction in quasi-extinction, but only the "70% preserved by area" and "maximum acquisition" have no quasi-extinction risk (Table 5-13b).

Recommendations: Comparison of simulations with equal population size but different spatial configuration (area vs. connectivity) indicates that maintaining contiguity of territories is more important than maintaining connectivity. Given this criteria, unprotected patches such as Jordan ("Brev31"), Valkaria ("Brev32"), Babcock ("Brev38"), and "Brev36" should be high priority acquisition sites. South of Sebastian along the coast the jay populations are in small, isolated populations that are extinction-prone. Acquisition of habitat (e.g. "InRi5") near the Wabasso Scrub Preserve ("InRi4") may bolster the long-term viability of that population. Significant numbers of unprotected jays occur along the Ten Mile Ridge in Indian River county ("InRi9" and "InRi10"), and other populations likely occur nearby (Breininger 1998), making this an important area for future acquisition. Habitat management plans are needed at the 3 airports known to have jays within this metapopulation (St. Lucie County, Sebastian Municipal, and Valkaria).

Recent surveys and color-band studies of "Brev30", "Brev31", "Brev32", "Brev35", "Brev36", "Brev37", and "Brev38" by Breininger (1998) documented an alarming population decline exceeding 50% since 1993. This decline is due primarily to habitat degradation resulting from fire suppression (Breininger 1998). An epidemic in late 1997-early 1998 also may have had a significant effect in this region (Breininger

1998). This population decline is not predicted by the model, and illustrates clearly the influence of the model parameter settings on the simulation results, which assume optimal habitat conditions. Similar declines likely are occurring in many other parts of the state, and highlight the importance of habitat restoration and management; land acquisition alone is insufficient to preserve jay populations.

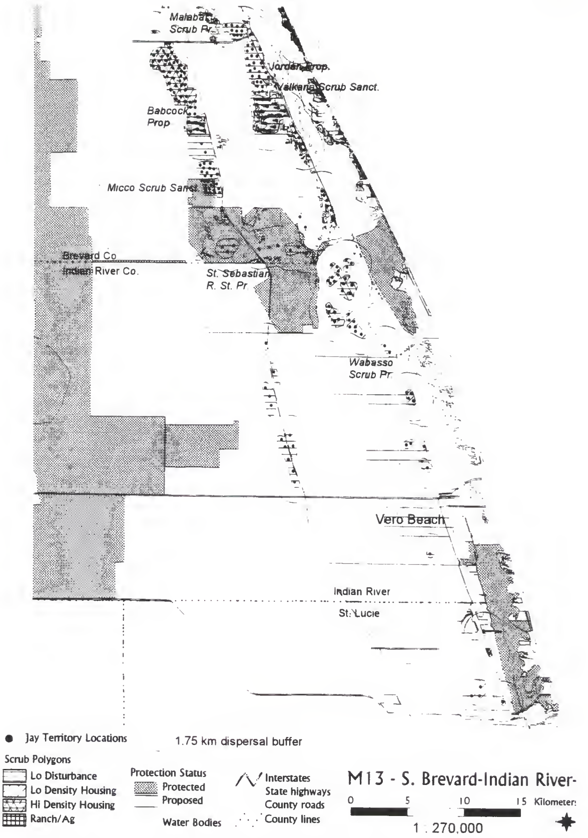


Fig. 5-13a. S. Brevard-Indian River-N. St. Lucie Metapopulation county map – 1992 - 1993 jay and habitat distribution.

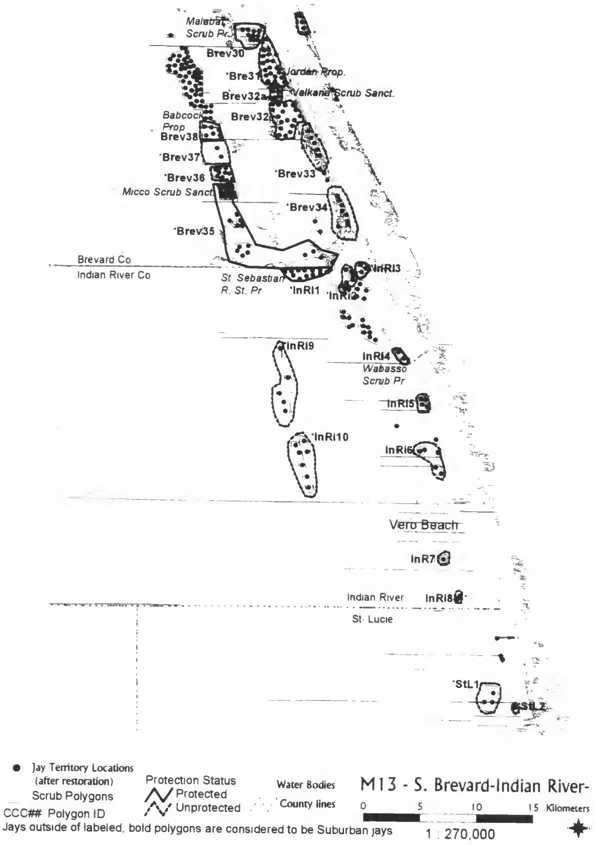
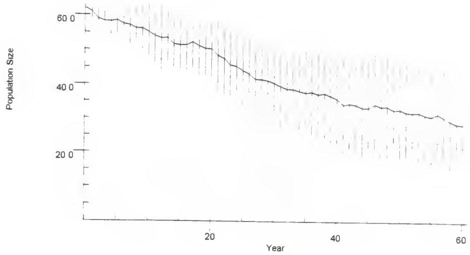


Fig. 5-13b. S. Brevard-Indian River-N. St. Lucie county acquisition map.

Table 5-13a. S. Brevard-Indian River-N. St. Lucie county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	30% preserved by connectivity	30% preserved by area	70% preserved by connectivity	70% preserved by area	Maximum acquisition
Brev30	Malabar Scrub Sanct.	10	10	10	10	10	10	10
Brev31	Jordan (proposed)	23		4	5	11	16	23
Brev32a	Valkaria (partial)	7	7	7	7	7	7	7
Brev32	(Valkaria - proposed)	17				9	17	17
Brev33		5		3		5	2	5
Brev34		8		5		7		8
Brev35	St. Sebastian River St. Pk. & Micco Scrub Sanct.	28	28	28	28	28	28	28
Brev36		11		3	11	6	11	11
Brev37		2		2		2	2	2
Brev38	(Babcock - proposed)	6		2	6	5	6	6
InRi1	St. Sebastian River State Park		12	12	12	12	12	12
InRi2	Sebastian municipal airport	8		5	8	8	8	8
InRi3	Private HCP	3	3	3	3	3	3	3
InRi4	Wabasso Scrub Pr.	2	2	2	2	2	2	2
InRi5		4				2		4
InRi6		5				2		5
InRi7		1				1		1
InRi8		2				2		2
InRi9		5		3		5	5	5
InRi10		7				5	7	7
StLu1	St. Lucie airport	3				2		3
StLu2		1				1		1
Totals		153	62	91	91	129	136	165



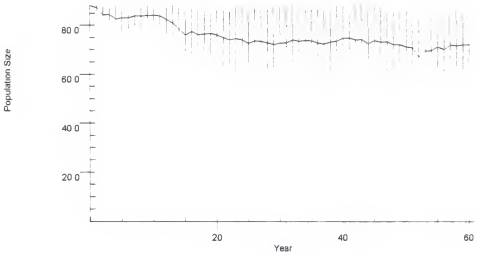
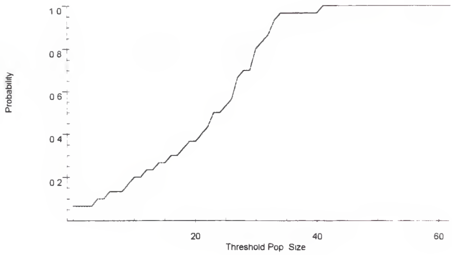


Fig. 5-13c. S. Brevard-Indian River-N. St. Lucie county trajectory graphs. Top) no acquisition, Bottom) 30% acquisition by area.



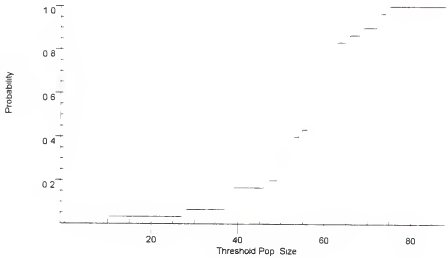


Fig. 5-13d. S. Brevard-Indian River-N. St. Lucie county quasi-extinction graphs. Top) no acquisition, Bottom) 30% acquisition by area.

Table 5-13b. S. Brevard-Indian River-N. St. Lucie county simulation statistics.

Data type	No acquisition	30% preserved by connectivity	30% preserved by area	70% preserved by connectivity	70% preserved by area	Maximum acquisition
Starting population size	62	91	91	136	136	165
Mean ending population size ± s.d.	28.5 13.5	44.3 17.9	71.9 13.9	91.1 21.4	107.3 15.3	124.1 15.0
Percent population decline	54.0	51.3	21.0	33.0	21.1	24.8
Extinction risk	0.07	0.0	0.0	0.0	0.0	0.0
Quasi-extinction Risk (10 pairs)	0.20	0.07	0.03	0.03	0.0	0.0

St. Lucie - N. Martin (M14)

General description: The St. Lucie-N. Martin metapopulation is separated from the S. Brevard-Indian River-N. St. Lucie metapopulation (M13) by the city of Fort Pierce to the north, and the Martin-N. Palm Beach metapopulation (M15) by the St. Lucie Inlet to the south (see map in Fig. 5-14a,b). The SMP documented about 28 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 23 pairs in currently protected areas, and 33 pairs maximum.

Protected areas: Savannas State Park ("Stl4"), and portions of the S. Savannas CARL site ("Mar1").

Restoration potential: The densities of jays measured by the SMP probably were close to maximum, even though habitat conditions were not optimal. For modeling purposes, the only population that was increased over the SMP was at Savannas State Park (15 pairs increased to 20).

Simulation results: This metapopulation ranked 12th in vulnerability (table 5-23), 7th in percent protected (62.2%; table 5-24), and 7th in priority (table 5-25), with high vulnerability and high potential for improvement. Quasi-extinction and extinction risk was substantially higher for the "no acquisition" option (p=0.73 and 0.20 respectively) compared to the the maximum acquisition option (p=0.27 and 0.03 respectively), even though the difference in population size was small (14 territories; Table 5-14b).

Recommendations: Habitat restoration and proper management of the Savannas State Park is crucial to this metapopulation. Acquisition of jay habitat within and south of the S. Savannas CARL site ("Mar1", "Mar2", "Mar3", "Mar4") will substantially

improve the long term prospects for this metapopulation. The status (and existence?) of the habitat patch ("Stl3") north of Savannas State Park and east of the county-owned Savannas Outdoor Recreation Area should be investigated.

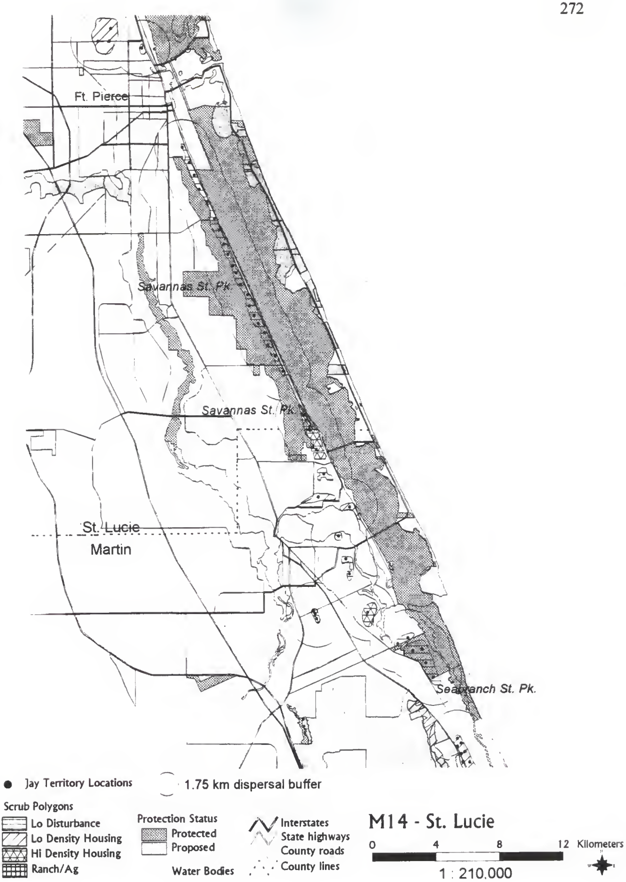


Fig. 5-14a. St. Lucie - N. Martin county map – 1992 - 1993 jay and habitat distribution.

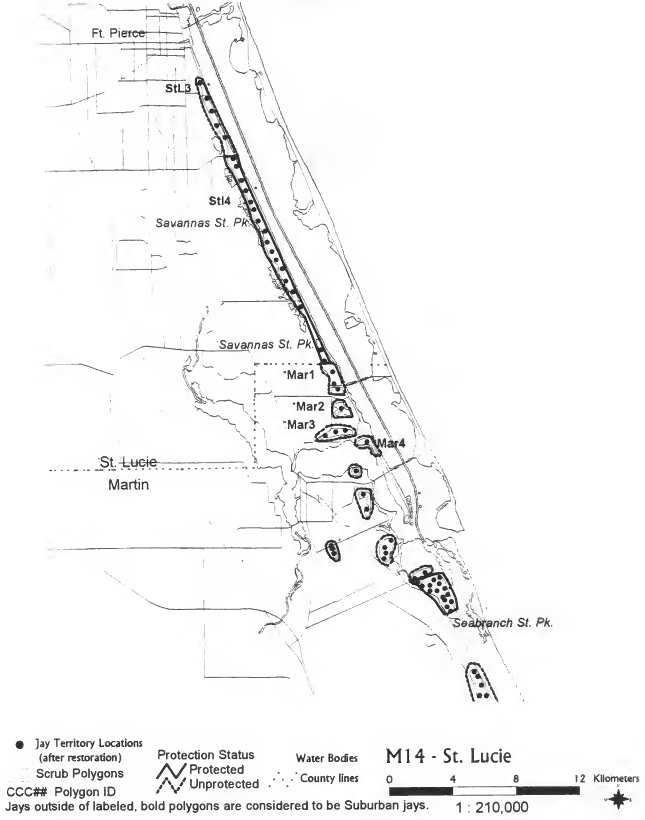
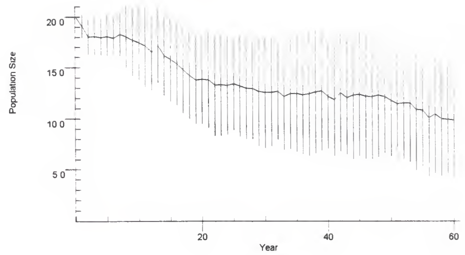


Fig. 5-14b. St. Lucie - N. Martin county acquisition map.

Table 5-14a. St. Lucie - N. Martin county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	Maximum acquisition
StL3		5		5
StL4	Savannas St. Pk.	15	20	20
Mar1	Private reserve	3	3	3
Mar2		1		1
Mar3		3		3
Mar4		1		1
Totals		28	23	33



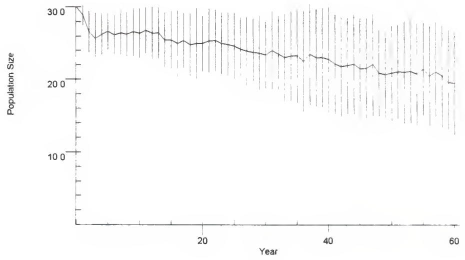
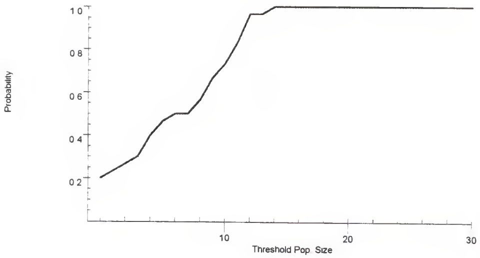


Fig. 5-14c. St. Lucie - N. Martin county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



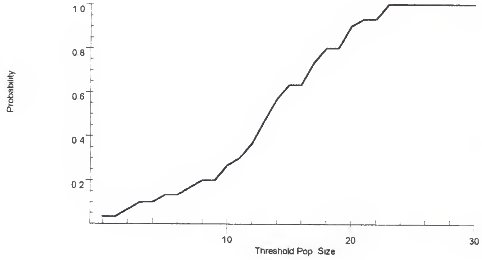


Fig. 5-14d. St. Lucie - N. Martin county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-14b. St. Lucie county simulation statistics

Data type	No acquisition	Maximum acquisition
starting population size	23	33
x end pop. size ± s.d.	9.8 5.9	19.4 7.1
percent decline	57.4	41.2
extinction risk	0.20	0.03
quasi-extinction risk (10 pairs)	0.73	0.27

Martin and N. Palm Beach (M15)

General description: The Martin-N. Palm Beach metapopulation is isolated from the St. Lucie-N. Martin metapopulation (M14) to the north by the St. Lucie Inlet, and is isolated from the South Palm Beach metapopulation (M16) to the south by heavy urbanization associated with West Palm Beach, Palm Springs, and Lake Worth. The SMP documented about 115 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 85 pairs in currently protected areas, and 120 pairs maximum.

Protected areas: Willoughby Dev. Preserve ("Mar7"), Seabranch State Park ("Mar10"), Jonathan Dickinson State Park ("Mar12"), F.P.L. Hill Station Preserve ("PB1"), St. Jude Scrub Jay Preserve ("PB3"), Jupiter Inlet Natural Area Preserve ("PB4"), Carlin County Park ("PB5"), Jupiter Ridge Natural Area ("PB6"), Juno Hills Natural Area Preserve ("PB8"), F.P.L. Universe Scrub Preserve ("PB9"). Portions of "Mar11" just north of Jonathan Dickinson State Park have been preserved through an HCP.

Restoration potential: The SMP estimates for Jonathan Dickinson State Park and Sea Branch State Park probably were erroneously high, but correspond well with what the densities would be after restoration and full occupancy. Restoration at Juno Hills Natural Areas Preserve might increase this population from the SMP estimate of 9 pairs to 14 pairs (Grace Iverson, pers. comm.).

Simulation results: This metapopulation ranked 18th in vulnerability (table 5-23), 4th in percent protected (70.8%; table 5-24), and 18th in priority (table 5-25), with low vulnerability and low potential for improvement. Extinction and quasi-extinction risk was

low, even for the “no acquisition” option. However, the mean percent population decline was substantially better for the “maximum acquisition” option (Table 5-15b).

Recommendations: The relatively favorable ranking of this metapopulation is due mainly to the significant jay populations at Jonathan Dickinson State Park, Sea Branch State Park, and Juno Hills Natural Area Preserve. The habitat quality for jays at all three of these parks reportedly is poor; restoration and proper management at these sites is vital to the viability of this metapopulation. Acquisition of unprotected habitat patches (“Mar15”, “PB6”, “PB7”) likely is important to the viability of nearby populations of jays that are already protected (e.g. Jupiter Ridge Natural Area, St. Jude Scrub Jay Preserve).

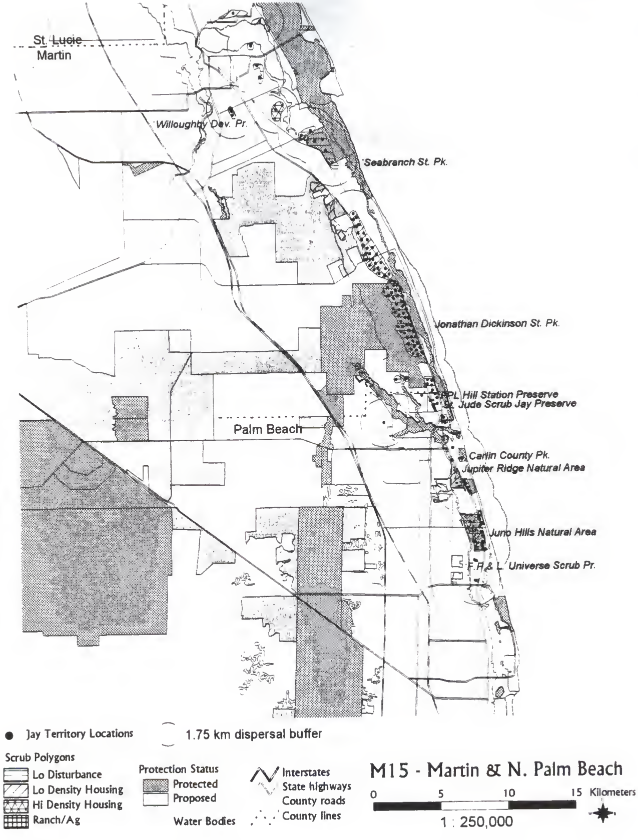


Fig. 5-15a. Martin and N. Palm Beach county map – 1992 - 1993 jay and habitat distribution.

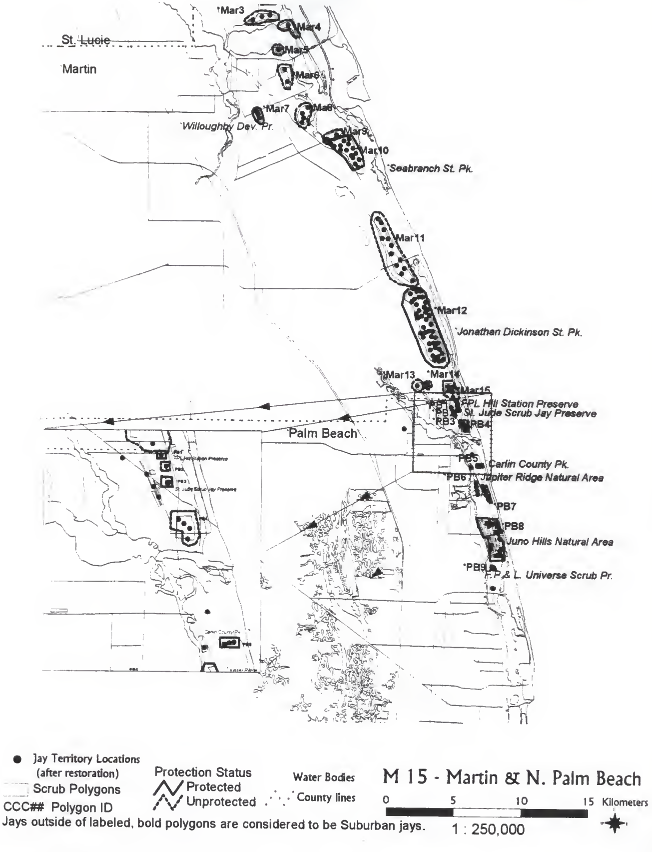
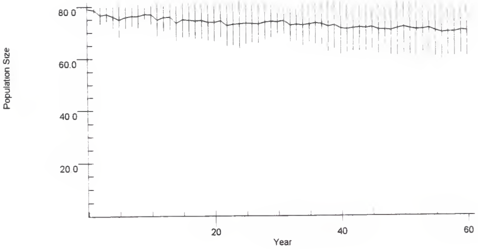


Fig. 5-15b. Martin and N. Palm Beach county acquisition map.

Table 5-15a. Martin and N. Palm Beach county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	Maximum acquisition
Mar5		1		1
Mar6		2		2
Mar7	Willoughby Dev. Pr.	3	3	3
Mar8		4		4
Mar9		2		2
Mar10	Seabranch St. Pk.	15	15	15
Mar11	(HCP)	12		12
Mar12	Jonathan Dickinson St. Pk.	40	40	40
Mar13		1		1
Mar14		1		1
Mar15		4		4
PB1	FPL Hill Station Pr.	1	1	1
PB2	(Tequesta Water Dept. - proposed)	1		1
PB3	St. Jude Scrub Jay Pr.	3	2	2
PB4	Jupiter Inlet Natural Area Pr.	3	4	4
PB5	Carlin County Pk.	3	3	3
PB6	Jupiter Ridge Nat. Area	4	4	4
PB7	(Radnor - proposed)	4		4
PB8	Juno Hills Natural Area Pr.	9	14	14
PB9	FPL Universe Scrub Pr.	2	2	2
Totals		115	85	120



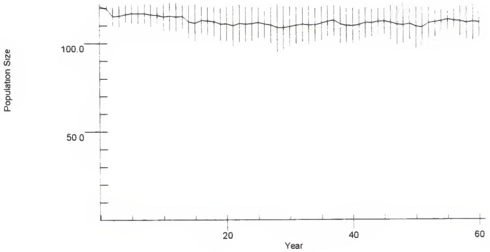
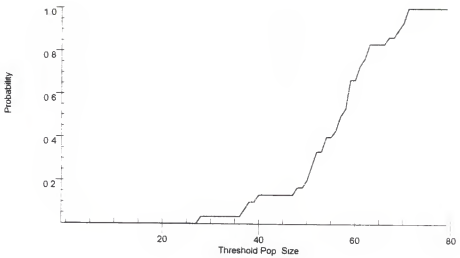


Fig. 5-15c. Martin and N. Palm Beach county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



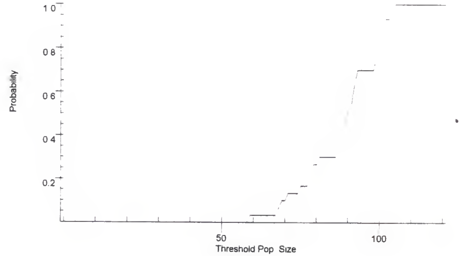


Fig. 5-15d. Martin and N. Palm Beach county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-15b. Martin and N. Palm Beach county simulation statistics

Data type	No acquisition	Maximum acquisition
starting population size	85	120
x end pop. size ± s.d.	70.3 10.0	111.3 8.6
percent decline	17.3	7.5
extinction risk	0.0	0.0
quasi-extinction risk (10 pairs)	0.0	0.0

South Palm Beach (M16)

General description: The South Palm Beach metapopulation is the most southerly metapopulation on the Atlantic coast. It is isolated from the Martin county metapopulation (M15) to the north by heavy urbanization associated with West Palm Beach, Palm Springs, and Lake Worth. All of the scrub patches are small and occur in suburban or urban settings. The SMP found 8 groups of jays, and characterized the condition of the scrub to be severely overgrown. The number of jays present during the SMP was only one-third the number found by Cox in 1980 (Pranty et al. manuscript). Estimated potential population size after habitat restoration and full occupancy is 9 pairs in currently protected areas, and 16 pairs maximum. Grace Iverson, who has studied jays in Palm Beach county for a number of years, provided invaluable information on this metapopulation.

Protected areas: Rolling Green Scrub Preserve ("PB11"), Galaxy School Scrub Preserve ("PB12"), Yamato Scrub NAP ("PB14"). A number of small scrub preserves that did not have jays during the SMP were excluded from all simulations (Osborne Scrub NAP, Gopher Tortoise Scrub NAP, Rosemary Ridge Scrub NAP, Leon Weeks Scrub Preserve NAP, Seacrest Scrub NAP, Rosemary Scrub NAP).

Restoration potential: The Yamato Scrub NAP ("PB14") had only 1 pair of jays during the SMP, but is estimated to potentially support about 6 pairs of jays if fully restored and managed.

Simulation results: This metapopulation ranked 8th in vulnerability (table 5-23), 6th in percent protected (69.2%; table 5-24), and 14th in priority (table 5-25), with high

vulnerability and low potential for improvement. Simulations of the "no acquisition" and "maximum acquisition" option both show a high quasi-extinction risk (p=1.0 for both) and a high extinction risk (p=0.90 and 0.77 respectively).

Recommendations: Because of the small size of this metapopulation and it's individual patches, and the heavily urbanized landscape which subjects these jays to additional sources of mortality, the long-term prognosis for this metapopulation is poor. An experimental program involving intensive human intervention might be necessary to maintain this metapopulation. Such a program likely would involve intensive habitat management, food supplementation, predator control, control of vehicular speed, and translocation of jays to supplement local population declines. No such program has been attempted for scrub-jays, but because of the huge human population in this area which could support and benefit from such a progam, this metapopulation might be the best candidate for such an experiment.

The two most significant habitat patches that remain unprotected include the Overlook Scrub ("PB14"), and the Tradewind / Winchester Site ("PB13"). Both of these patches occur near the already protected Rolling Green Scrub Preserve ("PB11") and Galaxy School Scrub Preserve ("PB12"). Acquisition and restoration of both of these sites would benefit the two nearby protected areas.

Fig 5-16a. Central Palm Beach county map – 1992 - 1993 jay and habitat distribution.

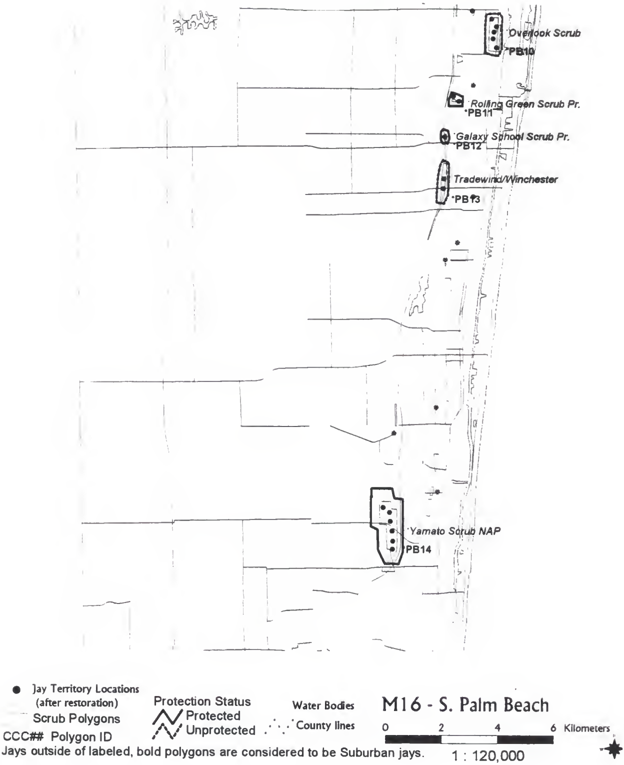
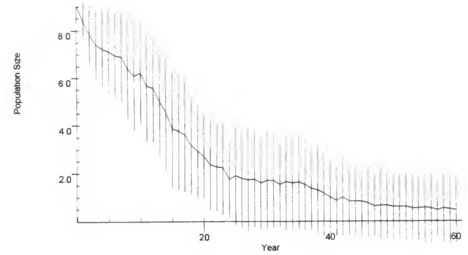


Fig. 5-16b. Central Palm Beach county acquisition map.

Table 5-16a. South Palm Beach county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	Maximum acquisition
PB10	(Overlook Scrub - proposed)	2		5
PB11	Rolling Green Scrub Pr.	2	2	2
PB12	Galaxy School Scrub Pr.	1	1	1
PB13	(Tradewind / Winchester Site)	2		2
PB14	Yamato Scrub NAP	1	6	6
Totals		8	9	16



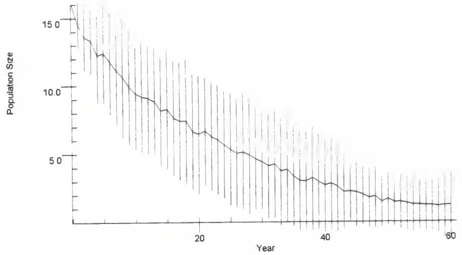
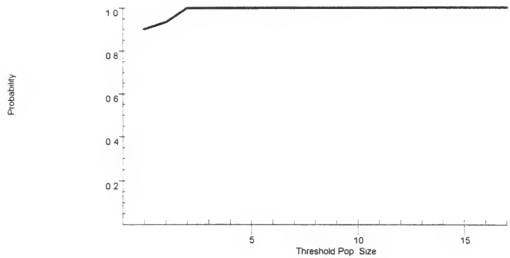


Fig. 5-16c. South Palm Beach county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



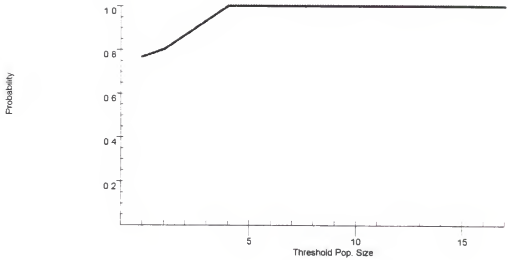


Fig. 5-16d. South Palm Beach county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-16b. South Palm Beach county simulation statistics

Data type	No acquisition	Maximum acquisition
starting population size	9	16
x end pop. size ± s.d.	0.47 1.34	1.20 2.40
percent decline	94.8	91.0
extinction risk	0.90	0.77
quasi-extinction risk (10 pairs)	1.0	1.0

Ocala National Forest (M17)

General description: The Ocala National Forest (ONF) metapopulation occupies most of W. Marion county and small portions of northeast Lake county. It is separated from the Central Lake metapopulation (M18) by major lakes (Lake Apopka, Lake Harris, Lake Dora, Lake Eustis, Lake Griffin, Lake Yale). The northeast Lake metapopulation (M18) to the southeast is separated from the ONF metapopulation by more than 30 km, with dense forest stands in between.

Protected areas: Most of this metapopulation is protected, occurring within the Ocala National Forest. During the SMP, an incomplete survey of the OCF population estimated this population at about 448 pairs. More recent surveys have increased this number considerably, to about 727 pairs (Laura Lowrie, pers. comm.).

Restoration potential: The restoration potential of the OCF population is enormous, since most of the extensive sand pine forest that is currently unoccupied could be restored to jay habitat. For modeling purposes, the population estimates given for the SMP were used (448 pairs).

Simulation results: This metapopulation ranked 20th in vulnerability (table 5-23), 1st in percent protected (table 5-24), and 20th in priority (table 5-25), with low vulnerability and low potential for improvement. Only a single simulation was run for this metapopulation, which assumed a starting population size of 470 pairs (Table 5-17a). This configuration had no risk of extinction or quasi-extinction, and showed a 25% mean population decline.

Recommendations: Despite the unusual management practice on ONF of creating temporary scrub jay habitat in small clearcuts within this extensive sandpine forest,

declines in jay populations have not been documented (Laura Lowrie, pers. comm.). Efforts are now being made to locate new clearcuts adjacent to recent openings to reduce fragmentation. The creation of a proposed 1900 acre parcel managed for scrub-jays and other fire-dependent scrub species should be of great benefit to this metapopulation.

Three small, unprotected jay populations occur outside the southwest portion of the ONF.

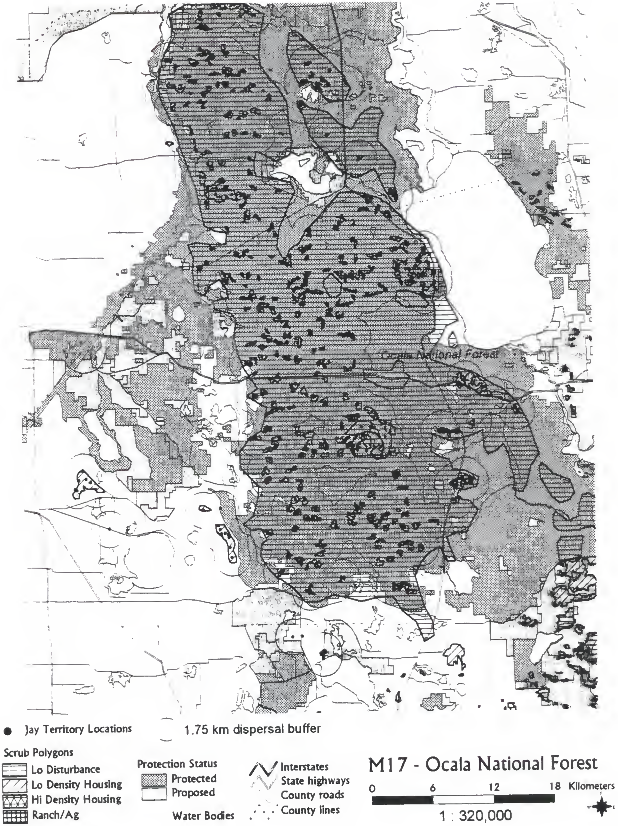


Fig. 5-17a. Ocala National Forest county map – 1992 - 1993 jay and habitat distribution.

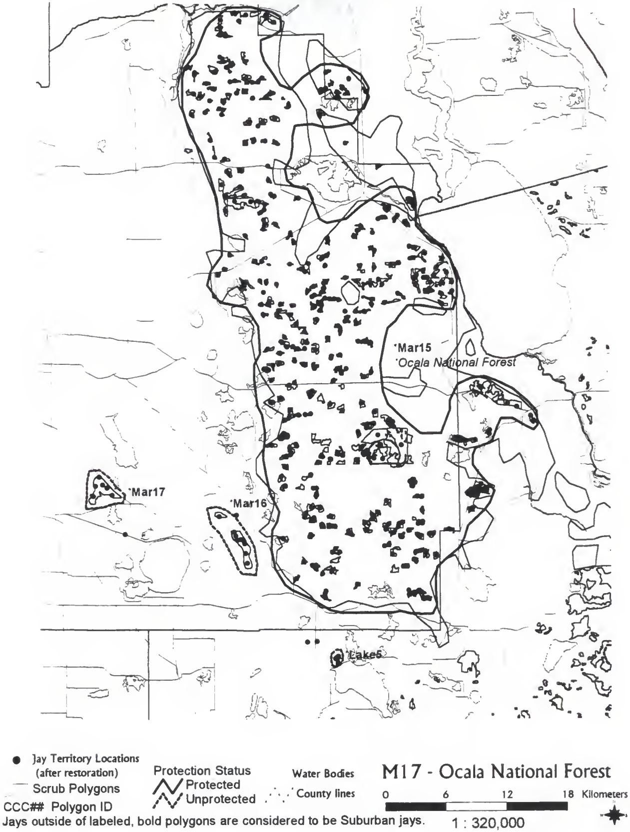


Fig. 5-17b. Ocala National Forest county acquisition map.

Table 5-17a. Ocala National Forest county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories
Mar15	Ocala National Forest	448
Mar16		9
Mar17		6
Lake5		7
Totals		470

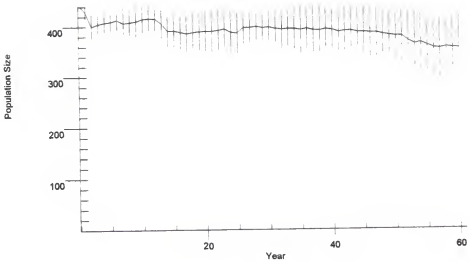


Fig. 5-17c. Ocala National Forest county trajectory graphs. No acquisition.

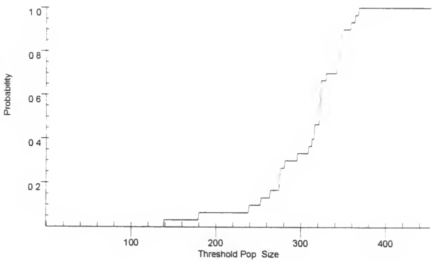


Fig. 5-17d. Ocala National Forest county quasi-extinction graphs. No acquisition.

Table 5-17b. Ocala National Forest county simulation statistics

Data type	Original 1992-1993 scenario
starting population size	470
x end pop. size ± s.d.	352.5 65.7
percent decline	25.0
extinction risk	0.0
quasi-extinction risk (10 pairs)	0.0

N.E. Lake (M18)

General description: The N.E. Lake metapopulation is separated from the W. Volusia metapopulation (M19) by the heavily wooded St. Johns riverine system to the west. The ONF metapopulation (M17) to the northwest is separated from the N.E. Lake metapopulation by more than 30 km, with an intervening matrix of dense forest stands. The SMP documented about 109 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 67 pairs in currently protected areas, and 161 pairs maximum.

Protected areas: Ocala N.F.("Lake11"), Seminole S. F. ("Lake7", "Lake8"), Rock Springs Run S.R. ("Ora2", "Lake6"), Wekiwa Springs S.P. ("Sem1", "Ora1"), Wekiva R. Buffers C.A. ("Sem1"), Yankee Lake Waste Water ("Sem3").

Restoration potential: Habitat patches in this metapopulation are heavily overgrown, and have an enormous potential for restoration. The largest patches of occupied habitat currently are unprotected ("Lake10", "Lake9"), and could support many more jays than were found during the SMP (compare the second and last data columns in Table 5-18a).

Simulation results: This metapopulation ranked 17th in vulnerability (table 5-23), 11th in percent protected (41.6%; table 5-24), and 17th in priority (table 5-25), with low vulnerability and low potential for improvement. The "no acquisition" option had a low risk of quasi-extinction (p=0.03), no extinction risk, and a 33.7% mean percent population decline (Table 5-18b). The "maximum acquisition" option has no risk of extinction or quasi-extinction, and a 10.9% mean percent population decline (Table 5-18b).

<u>Recommendations</u>: Habitat restoration is needed within most of the protected areas, and could substantially increase the size of this metapopulation.

More than half of the jays found during the SMP were in two large unprotected patches ("Lake9", "Lake10"), within or near the Royal Trails development. Acquisition of major portions of these patches would substantially improve the stability of this metapopulation.

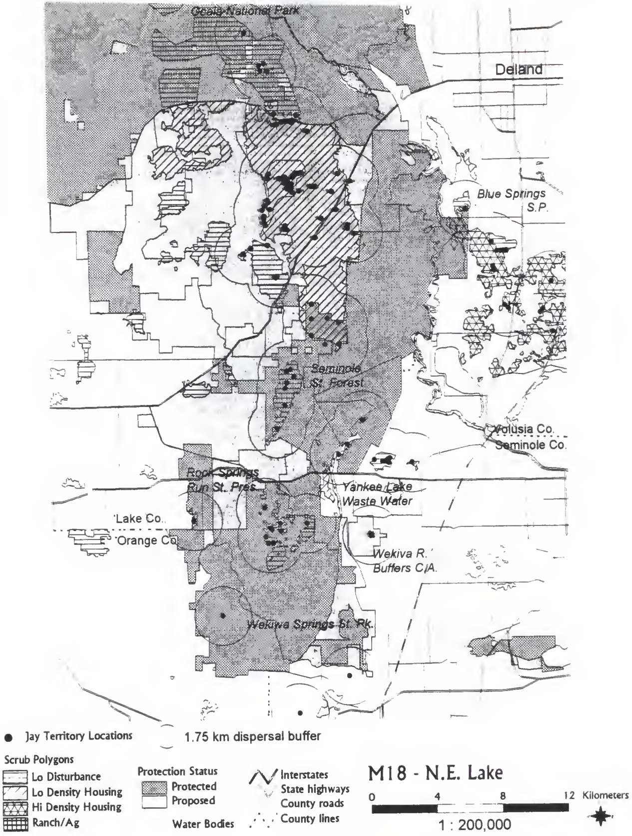


Fig. 5-18a. N.E. Lake county map – 1992 - 1993 jay and habitat distribution.

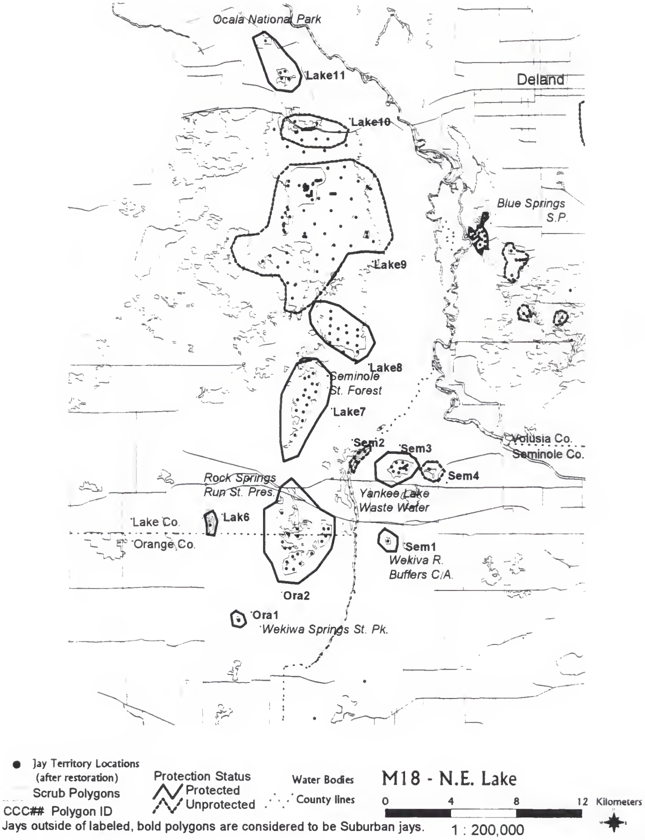
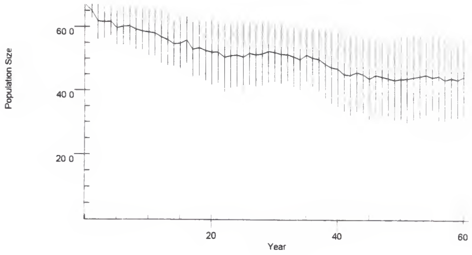


Fig. 5-18b. N.E. Lake county acquisition map.

Table 5-18a. N.E. Lake county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	Maximum acquisition
Lak6	Rock Springs Run S.R.	1	1	1
Lak7	Seminole S. F.	7	15	15
Lak8	Seminole S. F.	7	15	15
Lak9		56		71
Lak10		13		20
Lak11	Ocala N.F.	5	5	5
Ora1	Wekiwa Springs S.P.	1	1	1
Ora2	Rock Springs Run S.R.	9	19	19
Sem1	Wekiva R. Buffers C.A.	1	1	1
Sem2		2		2
Sem3	Yankee Lake Waste Water	6	10	10
Sem4		1		1
Totals		109	67	161



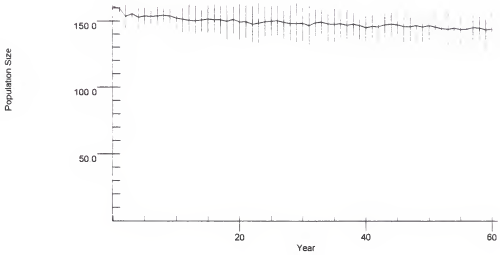
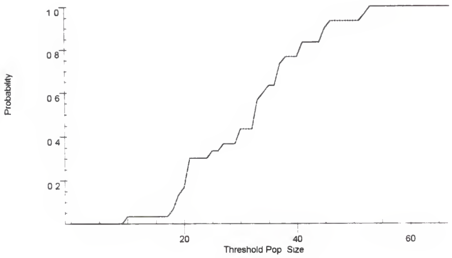


Fig. 5-18c. N.E. Lake county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



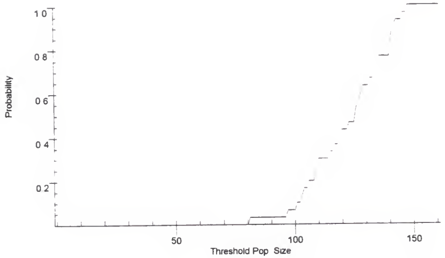


Fig. 5-18d. N.E. Lake county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-18b. N.E. Lake county simulation statistics

Data type	No acquisition	Maximum acquisition
starting population size	67	161
x end pop. size ± s.d.	44.4 12.9	143.8 14.5
percent decline	33.7	10.9
extinction risk	0.0	0.0
quasi-extinction risk (10 pairs)	0.03	0.0

S.W. Volusia (M19)

General description: The S.W. Volusia metapopulation is separated from the N.E. Lake metapopulation (M18) to the west by the St. Johns riverine system. The SMP documented about 54 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 17 pairs in currently protected areas, and 70 pairs maximum.

Protected areas: The only protected jays occur on the Blue Springs State Park ("Vol10" in Fig. 5-19b); a single family was found during the SMP.

Restoration potential: For modeling purposes, Blue Springs State Park was estimated to support 17 families of jays after restoration (probably an overly optimistic estimate). The largest population of jays occurs on the unprotected Stewart Ranch ("Vol19"), and this population likely could support more jays, but additional information is needed. Other patches in this metapopulation occur in the rapidly developing Deltona area south of Deland. The scrub in this area is heavily overgrown and the restoration potential is unknown.

Simulation results: This metapopulation ranked 11^{th} in vulnerability (table 5-23), 15^{th} in percent protected (24.3%; table 5-24), and 4^{th} in priority (table 5-25), with high vulnerability and high potential for improvement. The "no acquisition" option had a high risk of extinction (p=0.33) and quasi-extinction risk (p=0.90), and a 54.9% mean population decline (Table 5-19b). The "maximum acquisition" option had no risk of extinction or quasi-extinction, and a 20.2% mean population decline (Table 5-19b).

Recommendations: Near absence of protection for jays in this area combined with high potential to increase the protected population make this metapopulation high on the priority list. Three key responses to this situation are suggested . First, since Blue Springs is the only protected area with jays (one pair known from the SMP), all jay habitat should be restored as quickly as possible. Improved habitat data is needed to estimate the restoration potential of Blue Springs State Park. Second, unprotected, contiguous scrub habitat occurs north and east of the park (Fig. 5-19a); acquisition and restoration of these areas would bolster the local jay population.. Third, acquisition or protection of the large population of jays on the Stewart Ranch ("Vol19" in Fig. 5-19b) is critically important to this metapopulation.

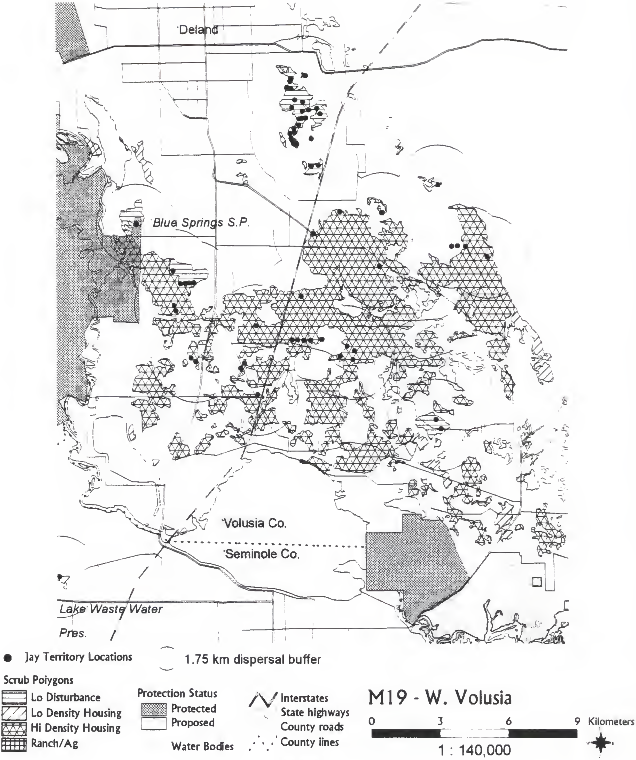


Fig. 5-19a. S.W. Volusia county map – 1992 – 1993 jay and habitat distribution.

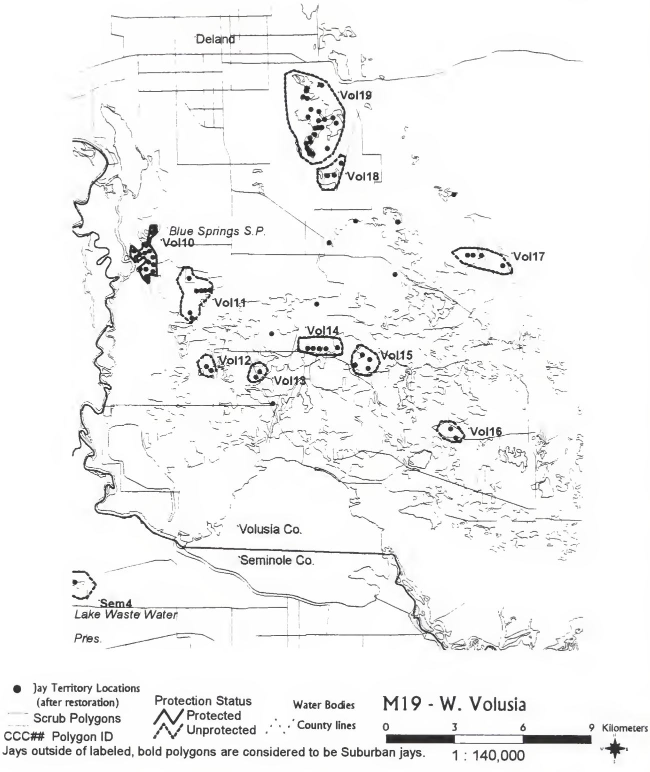


Fig. 5-19b. S.W. Volusia county acquisition map.

Table 5-19a. S.W. Volusia county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	30% preserved by contiguity	30% preserved by connectivity	70% preserved by contiguity	70% preserved by connectivity	Maximum acquisition
Vol10	Blue Springs S.P.	1	17	17	17	17	17	17
Vol11		7		3	3	7	5	7
Vol12		2		1	1	2	2	2
Vol13		2		1	1	1	2	2
Vol14		5		2	2		4	5
Vol15		4		1	1		3	4
Vol16		2		1	1		1	2
Vol17		4		1	1		3	4
Vol18		3		2	2	3	2	3
Vol19	Stewart Ranch (proposed)	24		4	4	24	15	24
Totals		54	17	33	33	54	54	70

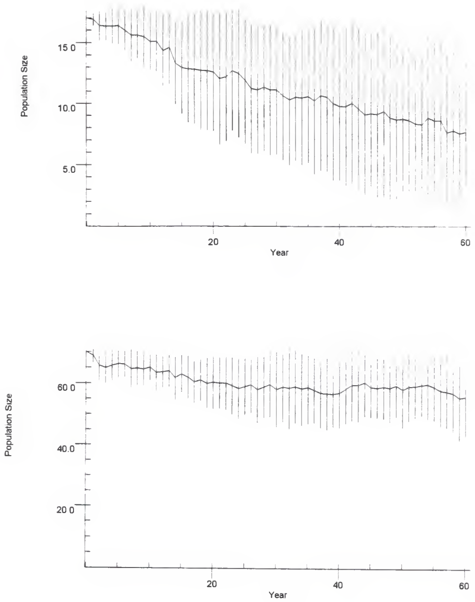
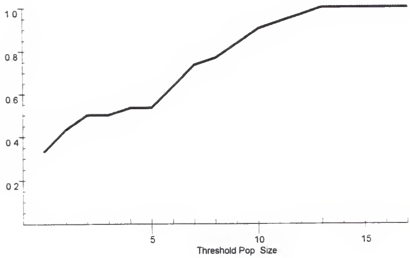


Fig. 5-19c. S.W. Volusia county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition



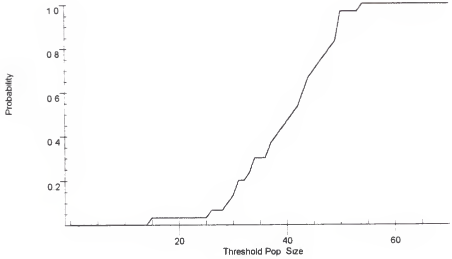


Fig. 5-19d. S.W. Volusia county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition

Table 5-19b. S.W. Volusia county simulation statistics

Data type	No acquisition (restored)	Maximum acquisition
Starting population size	17	70
Mean ending population size ± s.d.	7.67 6.22	55.87 13.3
% population decline	54.9	20.2
Extinction Risk	0.33	0.00
Quasi-extinction Risk (10 pairs)	0.90	0.00

Central Lake (M20)

General description: The Central Lake metapopulation (M20) is south of the Ocala National Forest metapopulation (M17) and west of the N.E. Lake metapopulation (M18). Major lakes in this area (Lake Apopka, Lake Harris, Lake Dora, Lake Eustis, Lake Griffin, Lake Yale) probably isolate these jays from the Ocala population to the north. The once extensive native upland areas in this region were converted decades ago to agriculture, and little native habitat remains. Only a few small patches of scrub remain, and some jays are living in scattered groups within abandoned citrus groves. The SMP documented about 13 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 0 pairs in currently protected areas, and 20 pairs maximum.

Protected areas: No jays occur in currently protected lands, with the possible exception of one group that may be using part of the Lake Apopka Restoration Area. Some scrub occurs adjacent to this property ("Lake2"), but it was excluded from the Water Management purchase. The habitat in "Lake2" and nearby "Lake3" potentially may support up to 10 pairs of jays (Table 5-20b).

Restoration potential: The restoration potential of this metapopulation is low; perhaps 20 pairs of jays could be protected under the maximum acquisition option (Table 5-20b).

Simulation results: This metapopulation is ranked 1st in vulnerability (table 5-23), last in percent protected (0.0%, table 5-24), and 14th in priority (table 5-25), with high vulnerability and low potential for improvement. Even the maximum acquisition option has a high risk of extinction (p=0.70) and quasi-extinction (p=1.0; Table 5-20b).

<u>Recommendations</u>: The best opportunity for protecting a small population of jays in this metapopulation probably lies in the acquisition and restoration of habitat near the Lake Apopka Restoration Area ("Lake2", "Lake3"). Jays found during the SMP at "Lake1" are in habitat proposed for acquisition; a search for additional nearby habitat may be worthwhile. A few unoccupied, heavily overgrown patches exist around lake margins in the northern portion of this metapopulation; jays potentially could be translocated to these sites if they were restored.

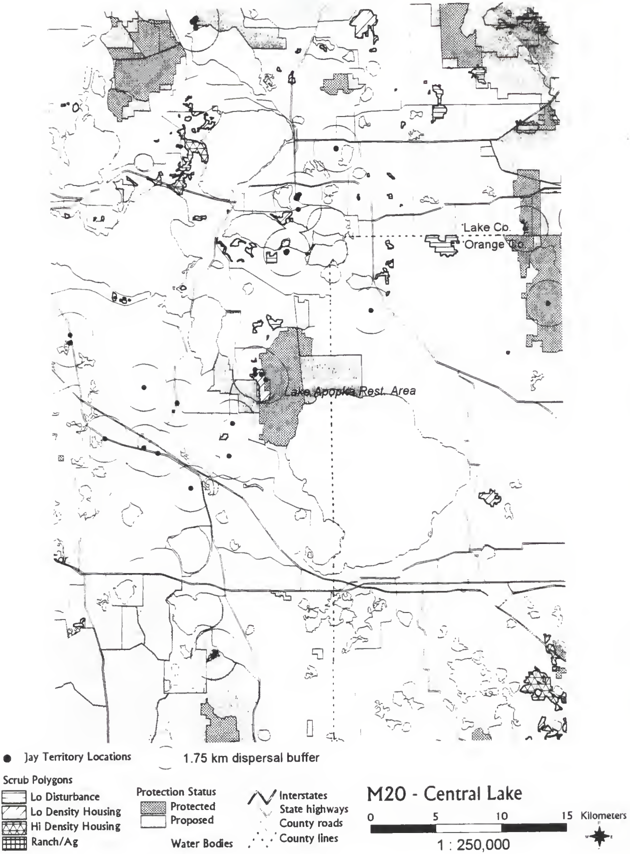


Fig. 5-20a. Central Lake county map – 1992 - 1993 jay and habitat distribution.

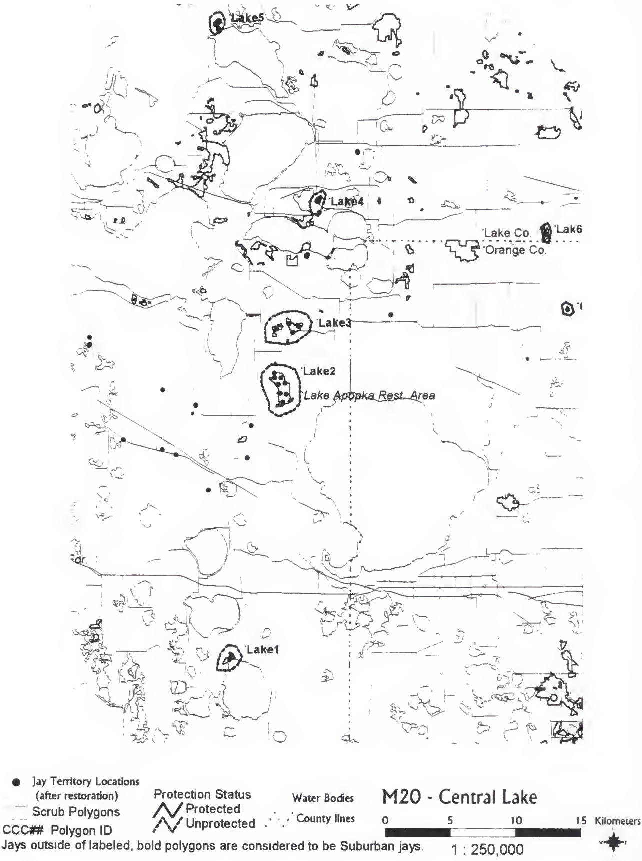
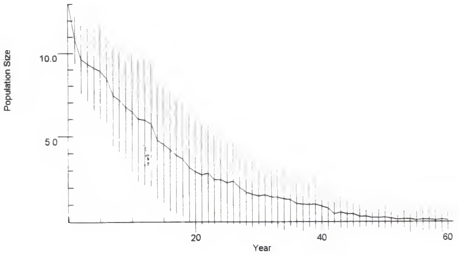


Fig. 5-20b. Central Lake county acquisition map.

Table 5-20a. Central Lake county patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	Maximum acquisition (restored)
Lake1		2		2
Lake2		4		8
Lake3		1		4
Lake4		6		6
Totals		13	0	20



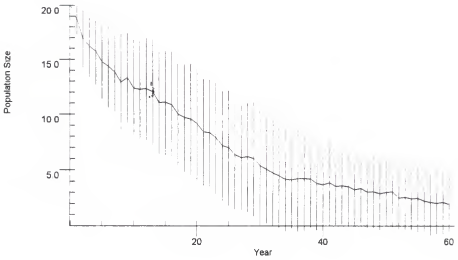
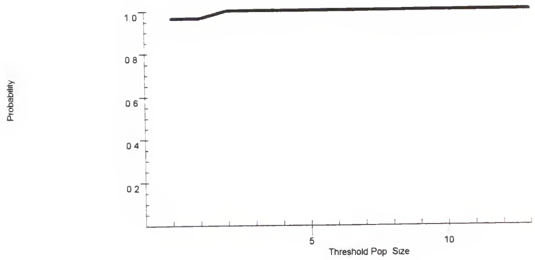


Fig. 5-20c. Central Lake county trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



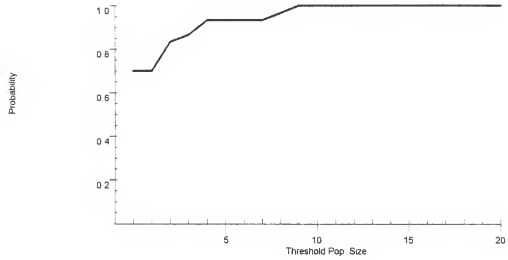


Fig. 5-20d. Central Lake county quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-20b. Central Lake county simulation statistics

Data type	Original 1992-1993 scenario	No acquisition	Maximum acquisition
starting population size	13	0	20
x end pop. size ± s.d.	0.10 0.60	--	1.93 2.9
percent decline	99.2	--	90.4
extinction risk	0.97	--	0.70
quasi-extinction risk (10 pairs)	1.0	--	1.0

Lake Wales Ridge (M21)

General description: The Lake Wales Ridge metapopulation is the largest metapopulation both in numbers of jays and in geographic extent. It's northern limit reaches into Orange county and extends southward through Polk, Highlands, and Glades county. The SMP documented about 565 jay territories, excluding suburban jays, in this metapopulation. Estimated potential population size after habitat restoration and full occupancy is 535 pairs in currently protected areas, and 858 pairs maximum.

Protected areas: Tiger Creek & Lake Wales S.F. (Polk6), Lk. Kissimmee S.P. (Polk10), Catfish Creek(Polk11), Disney Wilderness Pr. (Polk12), Platt Branch Mit. Pk. (High1), Archbold Biol. St. & Lake Placid W.E.A. (High4), Lake Wales Ridge W.E.A. (High7), Lake June Scrub S.P. (High11), Lake Wales Ridge W.E.A. (High13), Highlands Hammock S.P. (High15), Carter Creek(High17), Sun 'n Lakes (High19), Avon Park Air Force Range(Polk3). See Table 5-21a for tabulation of jay numbers.

Restoration potential: Much of the habitat in protected areas of this metapopulation has been or is being restored, but unprotected habitat is becoming increasingly overgrown. At the time of the SMP, jay densities in most areas were probably close to maximum (compare first and last data columns in Table 5-21a).

Simulation results: This metapopulation ranked 21st (last) in vulnerability (table 5-23), 5th in percent protected (62.3%; table 5-24), and 21st in priority (table 5-25), with low vulnerability and low potential for improvement. The "no acquisition" and "maximum acquisition" option both had no extinction or quasi-extinction risk, and had mean population declines of 18.5% and 17.4% respectively (Table 5-21b).

Recommendations: This metapopulation has been the focus of intensive acquisition efforts, and most major occupied habitat patches that are relatively undeveloped appear to be acquired or in the process of being acquired. However, none of the jays in Glades county are protected; many occur on the extensive landholdings of the Lykes Brothers Corporation. In Highlands county, the Hendrie Ranch ("High2") is an important unprotected population that doesn't appear on most acquisition lists. The jay population at Highlands Hammock State Park ("High15") is very small and somewhat isolated. Habitat restoration and additional acquisition is needed for this population. In Polk county, unprotected jay habitat ("Polk7") exists that would help connect Tiger Creek ("Polk6") and Catfish Creek ("Polk11"). The tiny population of jays at Lake Kissimmee State Park ("Polk10") would benefit from the acquisition of jays and habitat at "Polk8" and "Polk9". The most significant northerly population of jays occurs on the northeast margin of Lake Marion ("Polk13") on unprotected habitat, and doesn't appear on most acquisition lists.

Fig. 5-21a. Lake Wales Ridge map – overview.

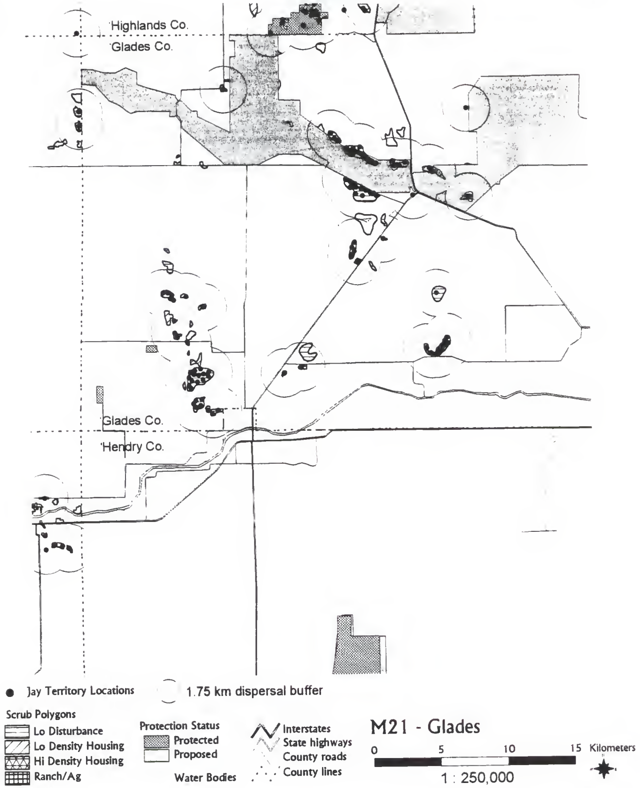


Fig. 5-21b. Lake Wales Ridge map – 1992 - 1993 jay and habitat distribution, Glades County.

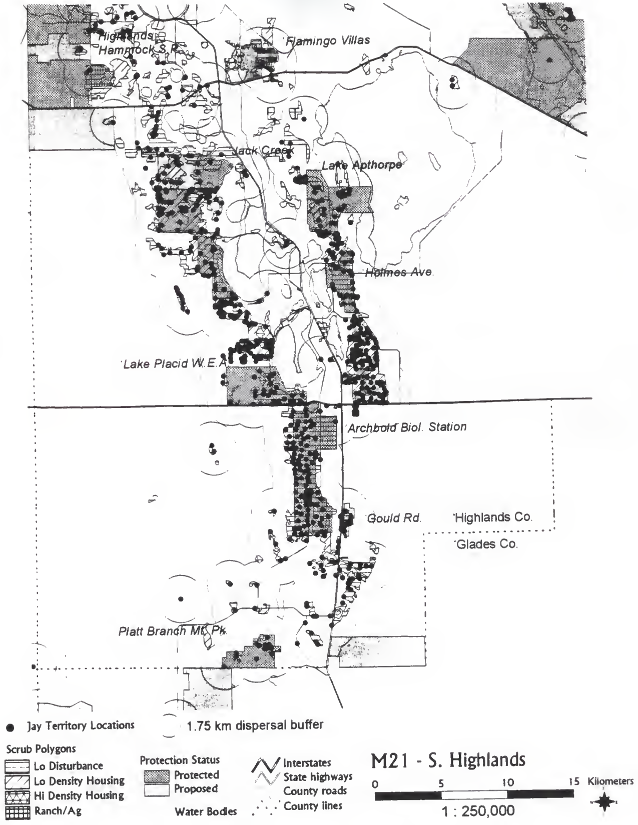


Fig. 5-21c. Lake Wales Ridge map – 1992 - 1993 jay and habitat distribution, S. Highlands county.

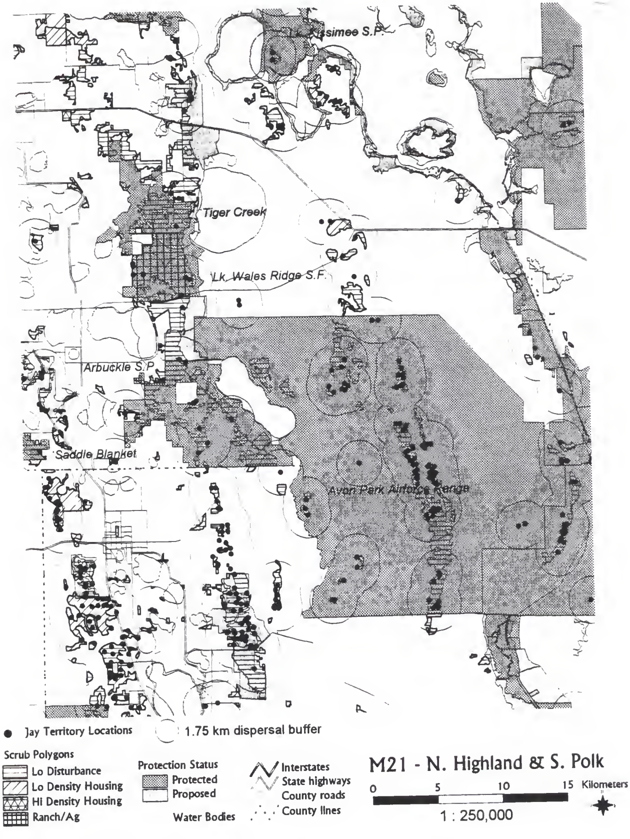


Fig. 5-21d. Lake Wales Ridge map – 1992 - 1993 jay and habitat distribution, N. Highlands and S. Polk county.

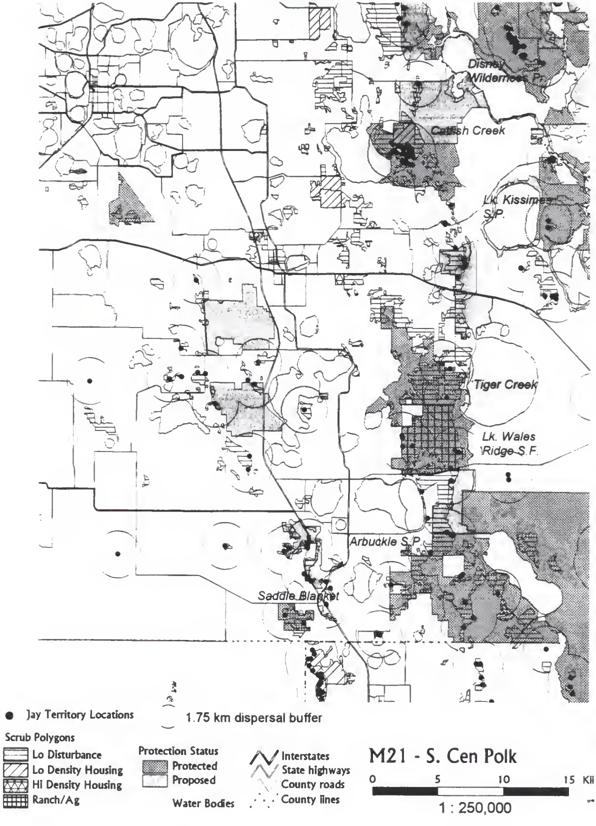


Fig. 5-21e. Lake Wales Ridge map – 1992 - 1993 jay and habitat distribution, S. central Polk county.

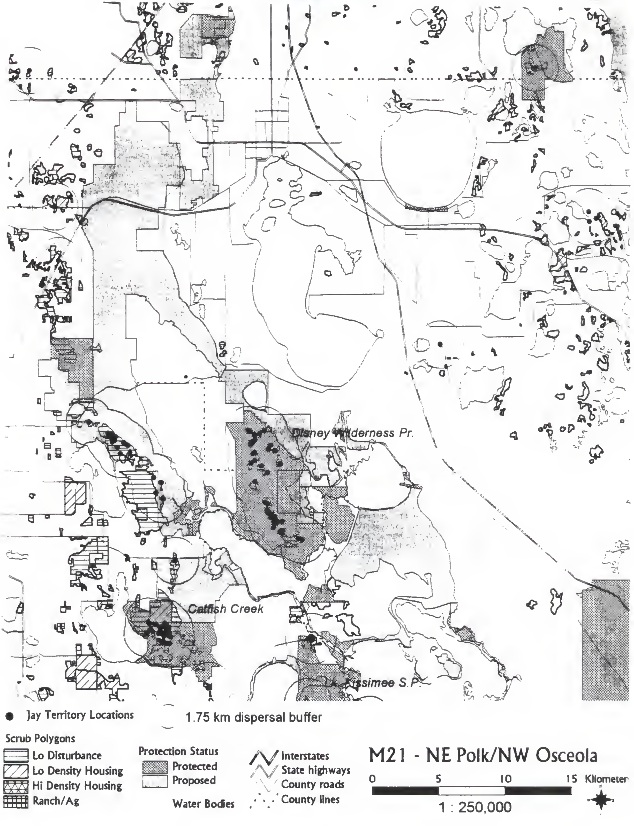


Fig. 5-21f. Lake Wales Ridge map – 1992 - 1993 jay and habitat distribution, N.E. Polk and N.W. Osceola county.

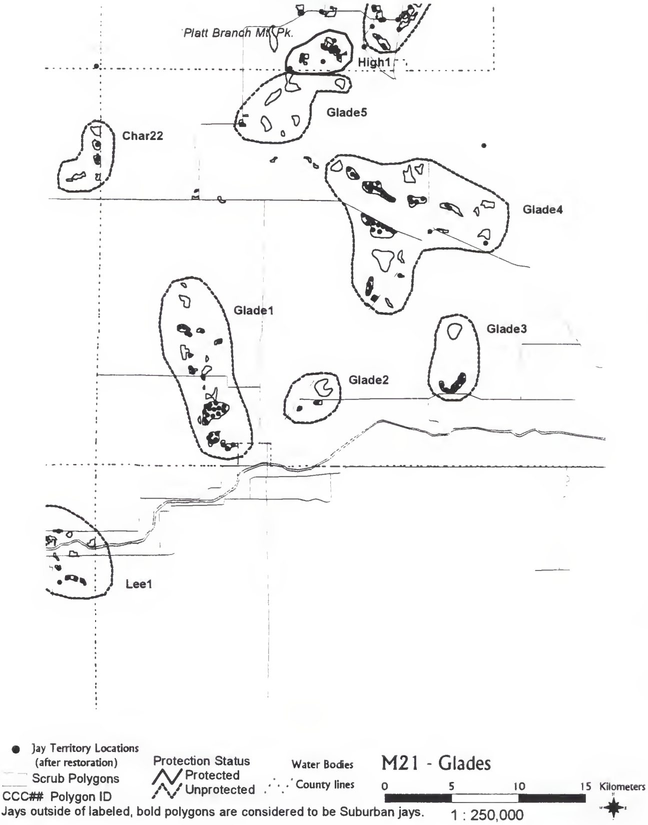


Fig. 5-21g. Lake Wales Ridge acquisition map, Glades county.

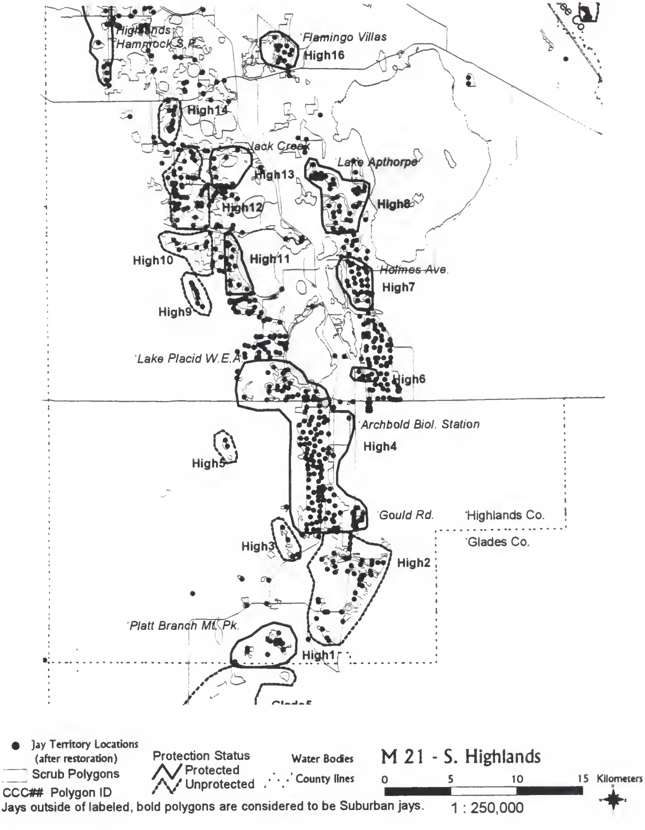


Fig. 5-21h. Lake Wales Ridge acquisition map, S. Highlands county.

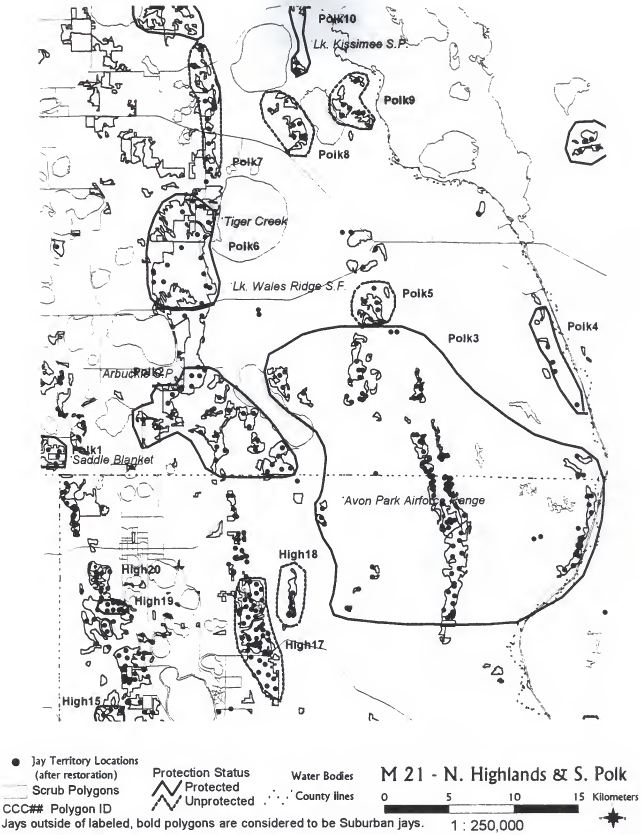


Fig. 5-21i. Lake Wales Ridge acquisition map, N. Highlands and S. Polk county.

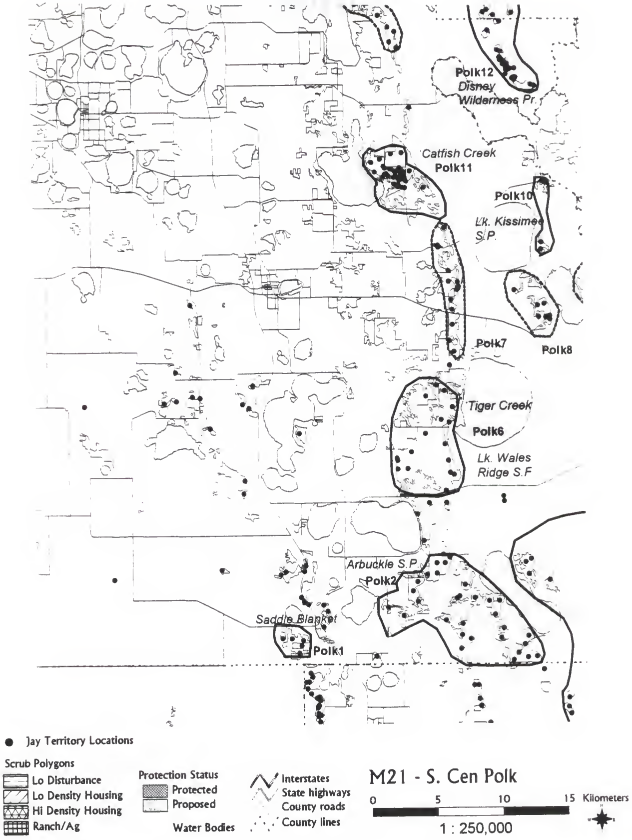


Fig. 5-21j. Lake Wales Ridge acquisition map, S. central Polk county.

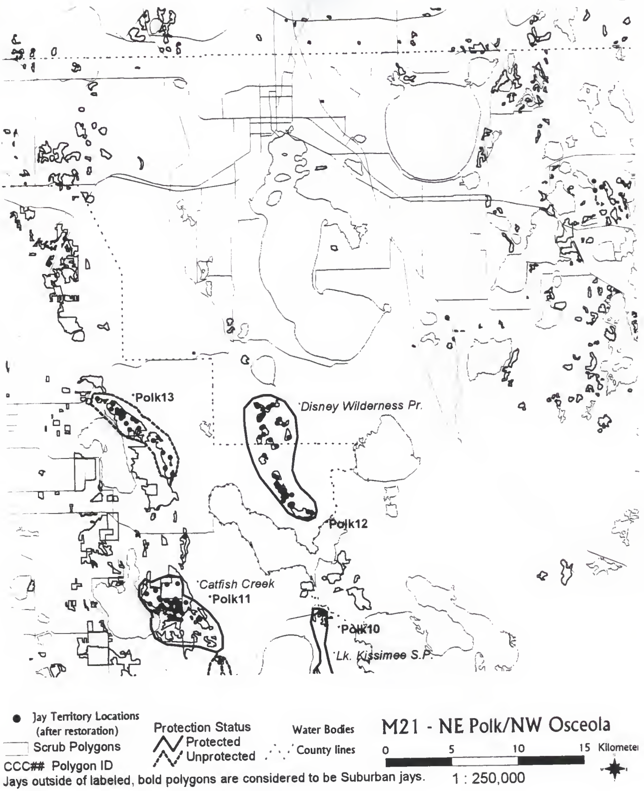


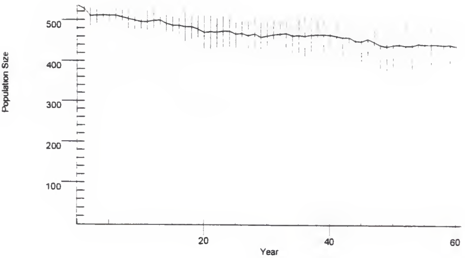
Fig. 5-21k. Lake Wales Ridge acquisition map, N.E. Polk and N.W. Osceola county.

Table 5-21a. Lake Wales Ridge patch statistics (number of jay territories for different configurations)

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	Maximum acquisition
Char22		2		2
Glade1		33		33
Glade2		2		2
Glade3		11		11
Glade4		41		41
Glade5		1		1
High1	Platt Branch Mit. Pk.	14	14	14
High2		40		40
High3		4		4
High4	Archbold Biol. St. & Lake Placid W.E.A.	141	134	141
High6	(proposed)	8	8	8
High7	Lake Wales Ridge W.E.A.	20	24	26
High8	Lake Wales Ridge W.E.A.	23	25	27
High9		8		8
High10		7		7
High11	Lake June Scrub S.P.	18	19	21
High12		30	28	30
High13	Lake Wales Ridge W.E.A.	10	8	10
High14		11		11
High15	Highlands Hammock S.P.	8	9	12
High16		7		12
High17	Carter Creek	36		48
High18		7		7
High19	Sun 'n Lakes	10		11
Okee1		11		11
Osc2		2	2	2
Polk1		2		5
Polk3	Avon Park Air Force Range	114	152	153
Polk4		4	4	4
Polk5		2		6

Table 5-21a - continued.

Patch id	Status	1992-1993 # jay territories	No acquisition (restored)	Maximum acquisition
Polk6	Tiger Creek & Lake Wales S.F.	11	17	17
Polk7		9		13
Polk8		6		8
Polk9		6		6
Polk10	Lk. Kissimmee S.P.	6	6	6
Polk11	Catfish Creek	34	41	41
Polk12	Disney Wilderness Pr.	39	39	39
Polk13		17		20
Totals		655	535	858



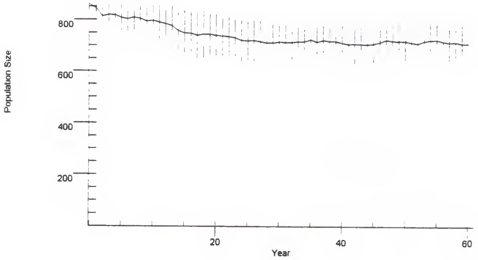
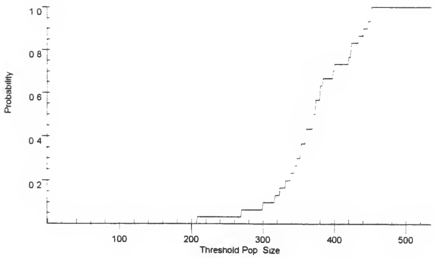


Fig. 5-211. Lake Wales Ridge trajectory graphs. Top) no acquisition, Bottom) maximum acquisition.



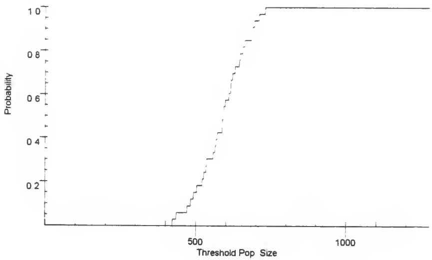


Fig. 5-21m. Lake Wales Ridge quasi-extinction graphs. Top) no acquisition, Bottom) maximum acquisition.

Table 5-21b. Lake Wales Ridge simulation statistics

Data type	No acquisition	Maximum acquisition
starting population size	535	858
x end pop. size ± s.d.	435.7 56.4	708.5 65.4
percent decline	18.5	17.4
extinction risk	0.0	0.0
quasi-extinction risk (10 pairs)	0.0	0.0

Other Metapopulations

Brevard barrier island

Jays on the Brevard barrier island have been studied intensively by Breininger (1999), who documented a precipitous decline since the SMP. These jays live in an urbanized matrix, and have very poor demographic performance. The demographic parameters measured by Breininger (1999) were used to parameterize suburban jays in all simulations (see Methods).

Clay county

Scrub-jays occur sporadically in Clay county, and have been seen most recently at Camp Blanding Military Reservation and along a powerline near Goldhead Branch State Park (Pranty et al. manuscript). These are the most northerly known jays in Florida's interior. Because they are fairly isolated from the nearest jay population in Ocala National Forest, they may be of interest genetically. Camp Blanding and Goldhead Branch have scrub that has been or is being restored. Natural recolonization may be a problem at these sites as the nearest significant population of jays is at Ocala National Forest. Translocation of jays might be worth investigating.

Osceola

A few jays are known to occur in scrub patches near Yeehaw junction and at scattered sites on the Osceola prairie to just north of St. Cloud. The SMP was not able to survey quite a few patches in this region, and it is likely that significant numbers of jays

occur in these patches and in unmapped habitat. *Additional surveys are urgently needed in this area.*

Western Polk

A few jays are known to occur in small scrub patches in southern Polk county to the west of the Lake Wales Ridge, several of which have been preserved for endemic plant species (e.g. Lake Blue and Lake McLeod), but are lacking scrub-jays. The western portion of Polk county has been heavily modified by the phosphate industry, and partially successful attempts have been made by industry to restore scrub or physically move scrub soils and vegetation. A few scrub-jays occur on these sites, and other jays undoubtedly occur on areas unsurveyed by the SMP.

Bright Hour Ranch

A substantial and apparently viable population of jays, estimated at 21 pairs during the SMP, exists in western DeSoto county at the Bright Hour Ranch. Now a conservation easement, this property is only 20 miles west of Archbold Biological Station. The jays at Bright Hour Ranch have a distinctive "hiccup" call (J. Fitzpatrick, pers. comm.; B. Stith, pers. obs.) which suggests that they may be highly isolated from the nearby jays on the Lake Wales Ridge.

Recommendations

Ranking Metapopulation Vulnerability

A summary of the primary metapopulation viability statistics produced by the simulations for each metapopulation is provided in Table 5-22. The metapopulations are not ranked in any meaningful order in this table. These are the raw values used in the analyses that follow.

Quasi-extinction risk (the probability of falling below 10 pairs) is used in this chapter as the primary statistic for ranking metapopulation vulnerability. A precedence exists for preferring quasi-extinction risk over extinction risk (the probability of total extinction) (see Stith et al. 1996; Breininger et al. in press). Other statistics such as population size and percent population decline also are used in these analyses, primarily to break ties for metapopulations having identical quasi-extinction risk.

Metapopulation viability ranking - no acquisition option. Table 5-23 provides a ranking of metapopulations based on vulnerability to quasi-extinction under the "no acquisition" option. This table provides a simple ranking of how vulnerable each metapopulation is if no further land acquisition occurs. The first 11 metapopulations on this list have a high quasi-extinction risk of 0.90 or greater (Central Lake, Central Charlotte, N. Brevard, Central Brevard, Levy, Manatee, Flagler, Palm Beach, Lee, N.W. Charlotte, and W. Volusia). These metapopulations warrant immediate attention, since without further acquisitions they are extremely vulnerable to quasi-extinction. At the bottom of the list, the last 5 metapopulations have a low probability of quasi-extinction, even without further acquisitions (N.E. Lake, Martin, Merritt Island, Ocala N.F., and

Lake Wales). However, interpretation of these low quasi-extinction probabilities must take into account the fact that this statistic is only sensitive to populations that decline below 10 pairs. Populations that have declined catastrophically, but not below 10 pairs, will not appear problematic using this statistic. Therefore, for these larger populations it is important to evaluate other statistics, such as percent population decline, and the mean-variance of the ending population size, which may reveal large declines in population size. One of the metapopulations that has a low quasi-extinction risk, N.E. Lake, has a large decline in population size (N.E. Lake: % decline = 33.7). Furthermore, none of the statistics presented here show which populations become extinct within each metapopulation. Examining the population persistence of specific key patches also may be important before concluding that a given metapopulation will not benefit significantly from further acquisitions.

Metapopulation viability ranking - maximum acquisition option. Although table 5-23 is helpful for identifying metapopulations most in need of further acquisition, it does not provide information on how much improvement in viability is potentially possible for a given metapopulation. Table 5-23a provides a ranking of metapopulation viability for the "maximum acquisition" option. Comparison of Tables 5-23 and 5-23a shows that the number of metapopulations with a quasi-extinction risk of 0.90 or greater is reduced from 11 to 5. The top three metapopulations appear to have little room for improvement. However, it may be inappropriate to "write-off" even these metapopulations, since unoccupied, restorable habitat may exist nearby, or the jays may warrant extreme intervention due to unique genetics, educational opportunities, or strong local support.

Percent population protected. Table 5-24 shows the percent of each population that is currently protected (assuming all habitat is restored and fully occupied). Eleven of the 21 metapopulations have less than 50% of their potential population protected.

Priority ranking. Table 5-25 provides a priority ranking of metapopulations based on a simple classification scheme I devised. The highest priority ranking is given to those metapopulations that are most vulnerable and have the highest potential for improvement. The lowest ranking is given to metapopulations with the lowest vulnerability and least potential for improvement. I arbitrarily defined three "vulnerability" categories based on the quasi-extinction estimate for the "no acquisition" scenarios (low vulnerability: $p = 0.0 - 0.05$, moderate vulnerability : $p = 0.5 - 0.20$, and high vulnerability: $p > 0.20$). I arbitrarily defined three "potential for improvement" categories based on the difference between the quasi-extinction estimates for the "maximum acquisition" option and the "no acquisition" option (low improvement: $p = 0.0 - 0.05$, moderate improvement : $p = 0.5 - 0.20$, and high improvement: $p > 0.20$).

This classification scheme indicates that there are 13 metapopulations of moderate or high vulnerability that also have moderate or high potential for improvement. These 13 metapopulations (N. Brevard, Levy, Central Charlotte, Central Brevard, W. Volusia, N.W. Charlotte, St. Lucie, Citrus, Lee, Manatee, Pasco, S. Brevard, and Sarasota) score highest on the priority list. Three metapopulations (Palm Beach, Central Lake, and Flagler) have high vulnerability, but low potential for improvement. The remaining 5 metapopulations have low vulnerability and low potential for improvement, at least as measured by quasi-extinction estimates. As discussed earlier, other statistics such as percent population decline should be used to evaluate these large metapopulations.

Summary of Recommendations

Table 5-26 lists each metapopulation in the order given by the priority ranking (table 5-25), and summarizes the recommendations provided earlier in each metapopulation section. Unprotected habitat patches with a high priority for acquisition are listed in the "Primary Acquisition Target" column; patches that may be of lower priority are listed in the "Secondary Acquisition Target" column. I decided which patches to place into the two acquisition categories subjectively, based on the results of different reserve design simulations and my overall impression from the modeling results that maintaining habitat contiguity is much more important than maintaining habitat connectivity. A systematic analysis of this contiguity vs. connectivity issue is needed. Habitat patches that are already protected but are in immediate need of restoration and management are listed in the "Restoration" column. The last column, "Other actions", lists miscellaneous activities that are recommended, such as additional surveys.

Table 5-22. Metapopulation viability statistics.

Metapopulation	Protected population size	Maximum population size	Extinction prob. (no acquisition)	Extinction prob. (maximum acquisition)	Quasi-ext. prob. (no acquisition)	Quasi-ext. prob. (maximum acquisition)	% decline (no acquisition)	% decline (maximum acquisition)
M1 - Levy	17	75	1.0	0.0	1.0	0.0	100.0	1.3
M2 - Citrus	47	125	0.17	0.0	0.47	0.33	70.6	55.0
M3 – Pasco	63	69	0.03	0.0	0.30	0.233	67.9	68.2
M4 – Manatee	36	145	0.97	0.30	1.0	0.90	95.3	96.6
M5 – Sarasota	50	89	0.03	0.0	0.10	0.0	47.4	47.3
M6 – N.W. Charlotte	28	56	0.67	0.07	1.0	0.30	91.8	60.7
M7 – Cen. Charlotte	5	61	1.0	0.07	1.0	0.07	100.0	65.4
M8 – Lee	15	62	0.73	0.40	1.0	0.90	92.7	90.9
M9 - Flagler	5	12	0.93	0.57	1.0	1.0	80.1	75.8
M10 – Merritt Island	495	536	0.0	0.0	0.0	0.0	0.70	6.5
M11 - N. Brevard	4	110	1.0	0.0	1.0	0.0	100.0	14.5
M12 – Cen. Brevard	5	40	1.0	0.0	1.0	0.10	100.0	36.3
M13 - S. Brevard	62	165	0.07	0.0	0.20	0.0	54.0	24.8
M14 – St. Lucie	23	37	0.20	0.03	0.73	0.27	57.4	19.4
M15 – Martin	85	120	0.0	0.0	0.0	0.0	17.3	7.5
M16 - Palm Beach	9	13	0.90	0.77	1.0	1.0	94.8	91.0
M17 – Ocala N.F.	448	???	0.0	0.0	0.0	0.0	25.0	???
M18 – N.E. Lake	67	161	0.0	0.0	0.03	0.0	33.7	10.9
M19 – W. Volusia	17	70	0.33	0.0	0.90	0.0	54.9	20.2
M20 – Cen. Lake	0	20	1.0	0.70	1.0	1.0	100.0	90.4
M21 – Lake Wales	535	858	0.0	0.0	0.0	0.0	18.5	17.4

Table 5-23. Metapopulation vulnerability ranking – "no acquisition" (sorted by decreasing quasi-extinction probability).

Rank	Metapopulation	Quasi-ext. prob. (no acquisition)	Extinction prob. (no acquisition)	Protected population size	Maximum population size
1	M20 – Cen. Lake	1.0	1.0	0	20
2	M7 – Cen. Charlotte	1.0	1.0	5	61
3	M11 - N. Brevard	1.0	1.0	4	110
4	M12 – Cen. Brevard	1.0	1.0	5	40
5	M1 - Levy	1.0	1.0	17	75
6	M4 – Manatee	1.0	0.97	36	145
7	M9 - Flagler	1.0	0.93	5	12
8	M16 - Palm Beach	1.0	0.90	9	13
9	M8 – Lee	1.0	0.73	15	62
10	M6 – N.W. Charlotte	1.0	0.67	28	56
11	M19 – W. Volusia	0.90	0.33	17	70
12	M14 – St. Lucie	0.73	0.20	23	37
13	M2 - Citrus	0.47	0.17	47	125
14	M3 – Pasco	0.30	0.03	63	69
15	M13 - S. Brevard	0.20	0.07	62	165
16	M5 – Sarasota	0.10	0.03	50	89
17	M18 – N.E. Lake	0.03	0.0	67	161
18	M15 – Martin	0.0	0.0	85	120
19	M10 – Merritt Island	0.0	0.0	495	536
20	M17 – Ocala N.F.	0.0	0.0	448	???
21	M21 – Lake Wales	0.0	0.0	535	858

Table 5-23a. Metapopulation vulnerability ranking – "maximum acquisition" (sorted by increasing percent protection).

Rank	Metapopulation	Quasi-ext. prob.(maximum acquisition)	Extinction prob. (maximum acquisition)	Protected population size	Maximum population size
1	M16 - Palm Beach	1.0	0.77	9	13
2	M20 – Cen. Lake	1.0	0.70	0	20
3	M9 - Flagler	1.0	0.57	5	12
4	M8 – Lee	0.90	0.40	15	62
5	M4 – Manatee	0.90	0.30	36	145
6	M2 - Citrus	0.33	0.0	47	125
7	M6 – N.W. Charlotte	0.30	0.07	28	56
8	M14 – St. Lucie	0.27	0.03	23	37
9	M3 – Pasco	0.23	0.0	63	69
10	M12 – Cen. Brevard	0.10	0.0	5	40
11	M7 – Cen. Charlotte	0.07	0.07	5	61
12	M19 – W. Volusia	0.0	0.0	17	70
13	M1 - Levy	0.0	0.0	17	75
14	M5 – Sarasota	0.0	0.0	50	89
15	M11 - N. Brevard	0.0	0.0	4	110
16	M15 – Martin	0.0	0.0	85	120
17	M13 - S. Brevard	0.0	0.0	62	165
18	M18 – N.E. Lake	0.0	0.0	67	161
19	M10 – Merritt Island	0.0	0.0	495	536
20	M21 – Lake Wales	0.0	0.0	535	858
21	M17 – Ocala N.F.	0.0	0.0	448	???

Table 5-24. Percent protected ranking – (sorted by increasing percent protection).

Rank	Metapopulation	Percent protected (after restoration)	Protected population size	Maximum population size	Quasi-ext. prob. (maximum acquisition)	Extinction prob. (maximum acquisition)
21	M20 – Cen. Lake	0.0	0	20	1.0	0.70
20	M11 - N. Brevard	3.6	4	110	0.0	0.0
19	M12 – Cen. Brevard	12.5	5	40	0.10	0.0
18	M1 - Levy	22.7	17	75	0.0	0.0
17	M8 – Lee	24.2	15	62	0.90	0.40
16	M19 – W. Volusia	24.3	17	70	0.0	0.0
15	M4 – Manatee	24.8	36	145	0.90	0.30
14	M2 - Citrus	37.6	47	125	0.33	0.0
13	M13 - S. Brevard	37.6	62	165	0.0	0.0
12	M18 – N.E. Lake	41.6	67	161	0.0	0.0
11	M9 - Flagler	41.7	5	12	1.0	0.57
10	M6 – N.W. Charlotte	50.0	28	56	0.30	0.07
9	M5 – Sarasota	56.2	50	89	0.0	0.0
8	M14 – St. Lucie	62.2	23	37	0.27	0.03
7	M16 - Palm Beach	69.2	9	13	1.0	0.77
6	M21 – Lake Wales	62.3	535	858	0.0	0.0
5	M15 – Martin	70.8	85	120	0.0	0.0
4	M7 – Cen. Charlotte	82.0	5	61	0.07	0.07
3	M3 – Pasco	91.3	63	69	0.23	0.0
2	M10 – Merritt Island	92.3	495	536	0.0	0.0
1	M17 – Ocala N.F.	???	448	???	0.0	0.0

Table 5-25. Metapopulation priority ranking (sorted by decreasing priority).

Rank	Metapopulation	Vulnerability	Potential for improvement	Quasi-ext. prob. – no acquisition	Difference in quasi-ext. prob. (max – no acquisition)
1	M11 - N. Brevard	high	high	1.0	1.0
2	M1 - Levy	high	high	1.0	1.0
3	M7 – Cen. Charlotte	high	high	1.0	0.93
4	M12 – Cen. Brevard	high	high	1.0	0.90
5	M19 – W. Volusia	high	high	0.90	0.90
6	M6 – N.W. Charlotte	high	high	1.0	0.70
9	M14 – St. Lucie	high	high	0.73	0.43
7	M2 - Citrus	high	mod.	0.47	0.14
8	M8 – Lee	high	mod.	1.0	0.10
10	M4 – Manatee	high	mod	1.0	0.10
11	M3 – Pasco	high	mod.	0.30	0.07
12	M13 - S. Brevard	mod.	mod.	0.16	0.16
13	M5 – Sarasota	mod.	mod.	0.10	0.10
14	M16 - Palm Beach	high	low	1.0	0.0
15	M20 – Cen. Lake	high	low	1.0	0.0
16	M9 - Flagler	high	low	1.0	0.0
17	M18 – N.E. Lake	low	low	0.03	0.03
18	M15 – Martin	low	low	0.0	0.0
19	M10 – Merritt Island	low	low	0.0	0.0
20	M17 – Ocala N.F.	low	low	0.0	0.0
21	M21 – Lake Wales	low	low	0.0	0.0

Table 5-26. Summary of recommendations (highest priority first).

Metapopulation	**Primary Acquisition Targets**	**Secondary Acquisition Targets**	**Restoration (protected areas)**	**Other actions**
N. Brevard (M11)	Brev4 (Buck Lake), Brev7 (addition to South Lake), Brev8 (Seminole Ranch), Brev9, Brev10, Brev11, Brev12, Brev15, Brev16, Brev17, Brev18	Brev6, Brev13		New jay surveys needed at most acquisition sites
Cedar Key (M1)	Levy2 (as much as possible)		Levy1 (Cedar Key Scrub Preserve)	
Central Charlotte (M7)	Char17, Char18, Char15, Char14, Char19	Lee5	Char16	Surveys needed along Prairie and Shell Creek (Char17,18,20)
Central Brevard (M12)	Brev41, Brev42		Brev40 (Rockledge Scrub Pr.), Brev43 (Wickham County Pk.), Brev44 (Melbourne regional airport)	
W. Volusia (M19)	Vol19, Vol18, Vol11		Vol10 (Blue Springs)	Additions to Vol10 (Blue Springs)
N.W. Charlotte (M6)	Char8, Char7, Sar13 (expand), Sar11	Char10, Char11, Sar12	Char9 (Charlotte Harbor S.B. Pr.)	
St. Lucie-N. Martin (M14)	Mar1 (additions), Mar2, Mar3, Mar4		Stl4 (Savannas S.P.), Mar1	Investigate status of Stl3

Table 5-26 (cont.)

Metapopulation	Primary Acquisition Targets	Secondary Acquisition Targets	Restoration (protected areas)	Other actions
Citrus-S.W. Marion (M2)	Mar2, Mar8, Citr2 (Re-evaluate after new survey completed)	Citr5, Mar7 (Re-evaluate after new survey completed)	Citr1 (Crystal R. St. Buffer Pr.), Citr6, Mar5, Sumt1	Improved survey. Purchase/restore unoccupied patches e.g. N. side of Citr3 & Mar3
Lee-Collier (M8)	Coll1, Coll4, Coll5, Coll7,		Lee3 (Estero Bay Aquatic Pr.), Coll2 (Rookery Bay N. Estuarine Research R.), Coll3 (Immokalee airport)	Purchase/restore unoccupied patches south of Lee3
Manatee (M4)	Sar16, Man1, Man16, Man15, Man9, Man10, Man11, Man5, Har1 (Re-evaluate after new survey completed)	(Re-evaluate after new survey completed)	Sar15 (Myakka S.P.), Sar19 (Verna Wellfield), Man15 (Duette), Man12&16 (Beker), Man17-18 (Lake Manatee), Hill2-3 (Little Manatee), Hill8 (Balm-Boyette Scrub Pr.), Hill9 (Golden Aster Scrub Nature Pr.)	New survey (emphasize atypical habitat)
Pasco (M3)	Pas2 (Re-evaluate after new survey completed)	(Re-evaluate after new survey completed)	Her1 (Weeki Wachee), Pas1 (Starkey/Serenova), Pas3 (Cross-bar/ Al-bar), Pas5 (Alston Tract), Pas6 (Green Swamp W.M.A.)	New survey (emphasize atypical habitat)
S. Brevard (M13)	Brev31, Brev32, Brev38 Brev36, InRi9, InRi10, InRi5, InRi6		Brev30 (Malabar Scrub Sanct.), Brev31 (Valkaria), Brev35 (St. Sebastian River S.P.& Micco Scrub Sanct.), InRi1 (Sebastian airport), InRi2 (private), InRi4 (Wabasso Scrub Pr.), StLu1 (St. Lucie airport)	Survey for additional jays on south end of Ten Mile Ridge

Table 5-26 (cont.)

Metapopulation	Primary Acquisition Targets	Secondary Acquisition Targets	Restoration (protected areas)	Other actions
Sarasota (M5)	Char2, Char3, Char4, Sar3, Sar5, Sar10	Char5, Char6, Sar1, Sar2,	Sar7 (Casperson/Brohard), Sar4 (Lemon Bay Scrub C.P.), Char1 (Charlotte Harbor St. Buffer Pr.), Sar14 (Myakka St. Forest)	
Palm Beach (M16)	PB10 (Overlook Scrub), PB13 (Tradewind/ Winchester)		PB14 (Yamato Scrub NAP), PB11 (Rolling Green Scrub Pr.), PB12 (Galaxy School Scrub Pr.)	Evaluate genetics; consider translocation program for educational facilities
Central Lake (M20)	Lake2, Lake3	Lake4, Lake1		Restore abandoned citrus groves?
Flagler (M9)	Flag1, Flag2		Vol1 (N. Peninsula St. Rec. Area),	Evaluate genetics; Investigate unoccupied inland habitat for translocation?
N.E. Lake (M18)	Lake9, Lake10		Lakd7 & Lake8 (Seminole St. Forest), Ora2 & Lake6 (Rock Springs Run S.Res.), Ora1 (Wekiwa Springs S.P.),	
Martin (M15)	Mar15, additions to Mar11, PB6, PB7		Mar12 (Jonathan Dickinson S.P.), Mar10 (Sea Branch S.P.), PB8 (Juno Hills N.A.P.), all other protected areas	
Merritt Island (M10)	Brev19, Brev20, Brev21, Brev22, Brev23		Brev25 (Merritt Island N.W.R. & Kennedy Space Center), Brev26 (Cape Canaveral Air Station)	

Table 5-26 (cont.)

Metapopulation	Primary Acquisition Targets	Secondary Acquisition Targets	Restoration (protected areas)	Other actions
Ocala National Forest (M17)			Creation of scrub-jay preserve in Mar15	
Lake Wales (M21)	High2 (Hendrie Ranch), High15 (additions to Highlands Hammock S.P.), Polk7, Polk8, Polk9, Polk13	all patches in Glades county?	High15 (Highlands Hammock S.P.), High17 (Carter Creek), High19 (Sun 'n Lakes)	

Discussion

Population viability analysis (PVA) models are coming under increasing criticism due to their sensitivity to questionable assumptions on model structure and their dependence on parameters for which field data are inadequate to define meaningful values (Karieva et al. 1997; Ludwig 1999). Examples of problematic model assumptions include density dependence (Mills et al. 1996) and correlation of environmental variation (spatial and temporal) (Burgman et al. 1993). Problems more specific to spatially explicit models were discussed recently in a series of papers (Bart 1995; Conroy et al. 1995; Dunning et al. 1995; Turner et al. 1995). Strong criticisms of spatially explicit models were made recently by Wennergren et al. (1995) and Ruckeslhaus et al. (1997), with replies by Mooij and DeAngelis (1999) and South (1999). Beissinger and Westphal (1998) provide a careful review of PVA models, and propose important qualifiers for the proper use of such models. Chief among these is the admonition to "place very limited confidence in the extinction estimates generated by these models." (p. 832-833). Instead, modelers are advised to "evaluate relative rather than absolute rates of extinction" and "concentrate on how well potential management actions perform relative to the baseline of current conditions." (p. 833). Beissinger and Westphal (1998) seem to imply that all such viability estimates are unreliable, but this is hard to square with their admonition to "evaluate relative rather than absolute rates of extinction". The use of relative rates presupposes that any differences in the predicted rates are significant to the viability of a population. If the model predictions differ greatly from what actually would happen in the real population, the predicted differences may amount to nothing from a management standpoint (e.g. the population will go extinct regardless of which management actions

are taken). Furthermore, the assumption that relative ranking is robust to model inaccuracies apparently has yet to be tested, and it is not difficult to imagine situations where relative rankings could change substantially depending on model parameter settings. For example, when comparing the viability of two metapopulations, one occurring in a single large patch, the other occurring in several small, isolated patches, the assumptions made about dispersal, the spread of epidemics, the correlation of environmental stochasticity, etc. could alter the relative ranking of the two metapopulations' viability.

I argue that these criticisms of models are excessive and stem from an unrealistic view of models. It is a banal truism that all models are false; none are completely accurate representations of real systems. Even simple, closed systems studied by physicists cannot be accurately modeled except in a very restricted sense (Cartwright 1983; Giere 1999). The main issue is whether a given model is sufficiently accurate to meet a particular need (Rykiel 1994). For this chapter, highly accurate predictions of the fate of Florida Scrub-Jays were not needed. I am interested primarily in comparing gross trends in the trajectories of hypothetical populations that might exist if present habitat conditions were improved.

In all likelihood, jay habitat will not be restored as assumed by the reserve design scenarios. Continued fire suppression and difficulties associated with habitat restoration will result in much less restored habitat than assumed by the scenarios. Furthermore, even if jay habitat were restored, the model results probably overestimate the persistence of jays. This is because I chose slightly "optimistic" settings for two parameters to favor small populations. Best estimates of the strength and frequency of epidemics measured at

Archbold Biological Station (Woolfenden and Fitzpatrick 1991) drive all small populations rapidly to extinction, at least according to my model (manuscript in prep.) and the models of Root (1996) and Breininger et al. (in press). I used less draconian values (see Methods section) for epidemics, thus assuming that some small populations will not be subject to epidemics as severe as those observed at Archbold Biological Station. I can see no other explanation for the decades-long persistence of certain isolated, small populations such as the Bright Hour Ranch (DeSoto county). A second factor which I set to favor small populations is the proportion of nonbreeders that become floaters (see Methods section). I assumed that in small populations, jays are more likely to become floaters than in larger populations, as fewer breeding opportunities exist (e.g. Breininger 1999).

Other reasons exist for viewing the results of this chapter as underestimating extinction risk. Several potentially important factors were excluded from the model, including genetic factors (e.g. inbreeding effects), hurricanes, fire suppression, and road mortality. Relevant genetic data are mostly unavailable for Florida Scrub-Jays, and no previous model of the species has included genetic factors. Breininger et al. (in press) examined the influence of hurricanes, and concluded that they could have a substantial effect on coastal populations. Although fires are thought to have strong negative effects for many species (e.g. McCarthy 1996), Florida Scrub-Jay populations actually depend on fire to maintain high habitat quality (Fitzpatrick et al. 1996). Thus, the reduction of demographic success in scrub-jays due to fire suppression (Fitzpatrick and Woolfenden 1986) is a major problem that is ignored in the simulations performed for this chapter. Mumme et al. (in review) documented significant effects of road mortality on scrub-jays,

which may create source-sink dynamics along roads. The absence of these factors from my model provides further reason to view the model predictions as underestimating extinction risk.

Thus, the results presented in this chapter must be viewed with these biases and assumptions in mind. One of the important steps in the modeling process is to present the structure of a model and its assumptions explicitly, so that others can decide whether the results are useful (Rykiel 1994). Models are "assumption analyzers" (Bart 1995) – they provide a means of integrating empirical data, hypotheses, theories, and intuition into a formal framework that reveals the consequences of the underlying assumptions. In my estimation, the assumptions I made for the simulations presented in this chapter should be viewed as optimistic with regard to Florida Scrub-Jay viability. Therefore, the simulation results which are summarized below should be viewed as optimistic scenarios for Florida Scrub-Jay metapopulations.

Assuming that no additional scrub-jay habitat is protected, 11 of 21 metapopulations were estimated to be highly vulnerable to quasi-extinction (N. Brevard, Levy, Central Charlotte, Central Brevard, W. Volusia, N.W. Charlotte, St. Lucie, Citrus, Lee, Manatee, Pasco). Of these 11 metapopulations, the risk of quasi-extinction could be greatly reduced for 7 metapopulations by acquiring all or major portions of the remaining jay habitat (N. Brevard, Levy, Central Charlotte, Central Brevard, W. Volusia, N.W. Charlotte, St. Lucie). However, even after total acquisition Central Charlotte and N.W. Charlotte showed large mean population declines (65% and 61% respectively). The other 4 metapopulations (Citrus, Lee, Manatee, and Pasco) showed high quasiextinction vulnerability, and moderate potential for improvement through acquisition. However,

each of these metapopulations showed large mean population declines (55% - 97%), even after complete acquisition of remaining habitat. Considering only the population trajectory data for the 11 highly vulnerable metapopulations, only 4 (N. Brevard, Levy, W. Volusia, and St. Lucie) had mean population declines of 20% or less after total acquisition.

Two metapopulations were classified as moderately vulnerable with a moderate potential for improvement (S. Brevard and Sarasota). Both of these metapopulations had one or more fairly stable subpopulations in protection, but had substantial mean population declines under the no acquisition option (54% and 47% respectively), indicating that without further acquisition the rest of the metapopulation might collapse, leaving both metapopulations vulnerable to epidemics or catastrophes.

Three metapopulations were classified as highly vulnerable to quasi-extinction, but had low potential for improvement (S. Palm Beach, Central Lake, and Flagler). These small populations are embedded in urban or agricultural landscapes with little or no habitat to acquire or restore. The peripheral Flagler and S. Palm Beach metapopulations are on the extreme north and south ends of the scrub-jay's range and may warrant special attention due to genetic considerations. Unoccupied inland scrub may be suitable for translocating coastal jays in Flagler. The S. Palm Beach metapopulation may have special educational value due to its proximity to the huge S. Florida human population.

The remaining five metapopulations (N.E. Lake, Martin, Merritt Island, Ocala National Forest, and Lake Wales Ridge) were classified as having low risk of quasi-extinction. Two of these metapopulations (Martin; N.E. Lake) have significant mean

population declines under the no acquisition option (17% and 34% respectively); these declines could be improved considerably by additional acquisitions.

CHAPTER 6
SYNTHESIS

The technique developed in chapter 2 to classify the metapopulation structure of the Florida Scrub-Jay provided qualitative expectations about the viability of different types of metapopulations. For example, systems composed only of islands are more vulnerable than systems with midlands, which in turn are more vulnerable than systems with mainlands. However, the technique provides no quantitative estimates of the viability of different configurations. The individual-based model described in chapter 5 permits such viability estimates, and allowed an assessment to be made of the viability of the major scrub-jay metapopulations around the state.

The reserve design scenarios simulated in chapter 5 did not allow the landscape to change over time. In a theoretical paper, Fahrig (1992) argues that temporal changes in habitat (patch "lifespan") are likely to be much more important than spatial factors. She found that the temporal scale of dispersal (dispersal frequency) far outweighed the spatial scale (dispersal distance) in affecting population recovery from patch disturbance. The most applicable implication of this finding for Florida Scrub-Jays today is that given the relatively short life span of scrub patches under the current human-dominated regime of fire suppression, large numbers of dispersing jays exploring many areas are needed to find the few recently burned, unoccupied patches. The ability to move long distances is much less unimportant than the ability to send out many dispersers to canvass a large

area. Given the dependence of jays on fire, scrub may seem like an ephemeral habitat, but relative to the average life span of a jay high quality scrub patches actually have a long "life span" (Woolfenden and Fitzpatrick 1984, chapter 10), especially under natural fire regimes. Consequently, jays need not rely on frequent, long distance dispersal to locate new patches of high quality scrub created by fire. In the spatial model developed for Florida Scrub-Jays by Root (1998), recovery of newly restored habitat was slow, and maintaining high habitat quality was much more important for population persistence. Indeed, sophisticated modeling is unnecessary to show that a population of jays in poor habitat cannot persist; it is a mathematical necessity that a population will decline unless reproductive rates offset mortality rates. An examination of the demographic performance of jays living in poor habitat made this clear over a decade ago (Fitpatrick and Woolfenden 1986).

As habitat patches change over time, two factors become difficult to separate: habitat loss and habitat fragmentation. Based on a general simulation model, Fahrig (1997) argues that details of how habitat is arranged cannot usually mitigate the effects of habitat loss, and that current emphasis on spatial pattern of habitat may be misplaced and overly optimistic. She recommends that conservation efforts be directed foremost at stopping habitat loss and at habitat restoration. Decisions still must be made about which habitat losses to stop and which habitat patches to restore. The simulation model developed for this dissertation can address such questions. However, the use of simulation to guide all such decisions often may be unnecessary. In the next and final section of this dissertation, a set of principles are presented to help guide conservation of the Florida Scrub-Jay. These principles are "landscape rules" that encapsulate much of

the information gleaned from modeling performed for this dissertation and by previous modeling efforts.

Conserving Florida Scrub-Jay Metapopulations

Human-induced fragmentation and habitat loss already have split the Florida Scrub-Jay into numerous metapopulations that are now effectively isolated from one another. Further habitat loss will have the inevitable effect of driving each metapopulation down an ever-steepening gradient of endangerment: mainland-midland configurations will become midland-island ones, classical configurations will become nonequilibrium ones, which in turn are headed inexorably to extinction. At different stages of this process, conservation strategies should vary. For systems still containing mainlands, preserving the mainlands usually overrides other concerns, as these large subpopulations have the greatest role in persistence of the system. As mainlands are lost, and subpopulations shift towards configurations of islands and midlands, conservation emphasis should shift from maintaining area to maintaining connectivity. In this phase, priority should be placed on keeping contiguous territories together, preserving centrally located patches, and minimizing distances among patches, thereby facilitating philopatric dispersal and maintaining opportunities for recolonization or rescue (Hanski 1994). As patch size and connectivity both become problematic (i.e., approaching nonequilibrium configuration), drastic measures are appropriate, such as intensive habitat restoration, perhaps coupled with translocation and reintroduction as a substitute for natural dispersal.

To stave off the Florida Scrub-Jay's current slide down the endangerment gradient, the following 'landscape rules' should be applied to each metapopulation independently, as appropriate (modified from Stith et al. 1996):

1) Preserve the cores. Three large, geographically separate subpopulations still have sufficient size as of 1993 (Fig. 2-6) to be highly invulnerable to extinction except in the face of a major catastrophe. Habitat protection should be undertaken to ensure that these large subpopulations are not split into two or more smaller ones. Two of these core populations occur on federal land (Ocala National Forest; Merritt Island and Cape Canaveral), the third is largely on private land in the southern part of the Lake Wales Ridge. We emphasize that even these core populations are not invulnerable to extinction. Epidemics among Florida Scrub-Jays are known to occur, and can be severe (Woolfenden and Fitzpatrick 1991). Furthermore, the entire Merritt Island-Cape Canaveral population exists only a few meters above sea level, and the effects of a large hurricane or sea level changes could be devastating (Breininger et al. in press).

2) Preserve all potentially viable metapopulations. The most effective long-term insurance against extinction is to make every effort to spread the risk of catastrophe as widely as possible. Certain nonequilibrium metapopulations--those with few remaining jays and lacking restorable habitat--probably are not viable in the long run. These may not warrant expensive conservation efforts, unless they have special genetic uniqueness, or geographic or educational importance (e.g., Lesica and Allendorf 1995). Permitting the ultimate destruction of these metapopulations should, of course, be accompanied by commensurate mitigation measures carried out in more viable metapopulations. Although the focus here is on Florida Scrub-Jays, it also should be pointed out that the jay co-

occurs with numerous narrowly adapted, range-restricted scrub endemics (e.g., Christman and Judd 1990). Many of these species will automatically be preserved if the full jay distribution is maintained; others, however, will require habitat preservation in areas deemed nonviable for the jay.

3) Favor preservation of contiguous territories. Jays that exist in clusters of contiguous territories are less extinction-prone than populations of equivalent size that occur as noncontiguous territories. The risks associated with floater dispersal are high (chapter 4), and breeder vacancies that arise within contiguous territories can be found using the much less risky philopatric dispersal strategy. Currently, I can offer no minimum population size or distance thresholds as quantitative guidelines for what constitutes a stable cluster of contiguous territories. I suspect that epidemics are the critical factor for determining this threshold (assuming habitat quality is high), but further modeling is needed to come up with appropriate guidelines.

4) Prohibit the splitting of metapopulations. Habitat gaps larger than 12 km represent barriers to natural dispersal and recolonization (chapter 2). To maintain all existing metapopulations, therefore, *all habitat gaps must be kept well below this 12 km threshold.* Failure to do so would effectively split the system apart and create two smaller, hence less viable, systems. Because coastal populations of Florida Scrub-Jays are distributed in narrow strips parallel to the coast line (dune and shoreline deposits), they are especially vulnerable to being split as a result of elimination of small habitat patches.

The emphasis of this dissertation has been on the influence of spatial factors on metapopulation viability. Landscape rules integrate much of the information derived from previous chapters and prior research, in a form useful for conservation. There are,

however, additional rules of a non-spatial nature that should be added to the landscape rules. Among the possible candidates, nothing is more important than the effects of habitat quality. Florida Scrub-Jay populations will decline drastically and deterministically as habitat quality declines (Woolfenden and Fitzpatrick 1991; Root 1997). It is unfortunate for the Florida Scrub-Jay that fire suppression by humans has greatly reduced habitat quality in many areas. Thus, a rule to the effect that habitat quality should be maintained at a high level is an obvious addition to the landscape rules. Restoration efforts at Kennedy Space Center, Florida, suggest that the use of fire alone to restore densely overgrown coastal scrub oaks may be ineffective (D. Breininger, pers. comm.). Swain et al. (1995) suggest that unburned scrub close to public roads or with high pine canopy cover will be difficult to restore. The restoration experiment mentioned in chapter 3 suggests that jays may be reluctant to colonize newly restored, vacant habitat. Modeling results of Breininger et al. (in press) suggest that effective restoration depends on having a surplus of local helpers. Although much remains to be learned about habitat restoration, the selection of habitat patches to be restored clearly should take into account spatial factors, especially the proximity of healthy jay populations that can provide colonists to the habitat being restored.

The spatially explicit, individual-based modeling approach provides a powerful framework for investigating conservation issues in a repeatable, quantifiable fashion. The model I developed for this dissertation could be modified to incorporate features such as dynamically changing landscapes, fire, road effects, genetics, etc. The technology and programming tools are capable of this and much more. What is lacking is the necessary field data to calibrate and validate the model. Perhaps the biggest problem

facing these types of models is ascertaining the reliability of model predictions. Rykiel (1996) provides a general review of various means of model validation, and concludes that model validation has many different meanings and no standard methods. The use of postdiction or retrospective testing to compare historic data with model predictions has been used only occasionally for PVA models. Brook et al. (1997) documented the 10-year population trajectory of the Lord Howe Island wood hen following the release of 86 captive-bred individuals. Model predictions were unreliable unless accurate post facto estimates of carrying capacity were used. Intuitively, the strongest form of validation occurs when model predictions are not falsified by future events. This strong form of model validation, the statistical comparison of predicted and actual trajectories, requires long term data replicated in different areas for different landscapes. Obtaining such data may be impossible for most species, but substantial data sets for at least 6 different color-banded populations of Florida Scrub-Jays (Archbold Biological Station, Lake Placid, Avon Park Air Force Range, Sarasota county, S. Brevard county, and Kennedy Space Center) are already available, and coarser survey data for other parts of the state also are available. Stable and declining population trajectories have been documented in these areas, and offer an excellent opportunity to further test and refine this model. It is my hope to continue working on this model and intriguing species, the Florida Scrub-Jay, for which so much is known, but so much more remains to be discovered.

REFERENCES

Abrahamson, W.G., A.F. Johnson, J.N. Layne, and P.A. Peroni. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. Florida Scientist 47: 209-250.

Akcakaya, H.R. 1994. RAMAS/GIS: Linking Landscape Data with Population Viability Analyses (version 1.0). Setauket, New York: Applied Biomathematics. 230 pp.

Akcakaya, H.R. and J. Atwood. 1997. A habitat-based metapopulation model of the California Gnatcatcher. Conservation Biology 11: 422-434.

Akcakaya, H.R. and S. Ferson. 1990. RAMAS/space User Manual: Spatially-structured Population Models for Conservation Biology. Setauket, New York: Applied Biomathematics. 83 pp.

Anderson, P.K. Dispersal in Rodents: A Resident Fitness Hypothesis. Special publication no. 9. The American Society of Mammalogists. 139 pp.

Anonymous, 1999. Conservation and recreation lands program annual report. Office of Land Use Planning and Biological Services, Florida Department of Natural Resources, Tallahassee, Florida.

Barrowclough, G.F. 1978. Sampling bias in dispersal studies based on finite area. Bird-Banding 49: 333-341.

Bart, J. 1995. Acceptance criteria for using individual-based models to make management decisions. Ecological Applications 5: 411-420.

Batschelet, E. 1981. Circular Statistics in Biology. Academic Press, New York. 371 pp.

Beier, P. 1996. Metapopulation models, tenacious tracking, and cougar conservation. Pages 293-324 in D. McCullough (ed.), Metapopulations and Wildlife Conservation. Washington DC: Island Press. 429 pp.

Bell, W.J. 1991. Searching behaviour: the Behavioural Ecology of Finding Resources. New York: Chapman and Hall. 358 pp.

Beissinger, S.R. and M.I. Wesphal. 1998. On the use of demographic models of population viability in endangered species management. J. Wildlife Management 62: 821-841.

Best, L.B., and D.F. Stauffer. 1986. Factors confounding the evaluation of bird-habitat relationships. Pages 209-217 in J. Verner, M.L. Morrison, and C.J. Ralph (eds.), Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. Madison: University of Wisconsin Press.

Blanchard, J., S. Jue, and A. Crook. 1998. Florida Conservation Lands 1998.

Bowman, R. and L. Averill. 1993. Demography of a suburban population of Florida Scrub Jays. Annual Progress Report to the U.S. Fish and Wildlife Service.

Boyce, M.S. 1992. Population viability analysis. Ann. Rev. Ecol. Syst. 26: 481-506.

Breininger, D.R. 1999. Florida Scrub-Jay demography and dispersal in a fragmented urban landscape. Auk 116: 520-527.

Breininger, D.R. 1997. Florida Scrub-Jay demography in an urban metapopulation. 1997 Final Report to Endangered Species Office, U.S. Fish and Wildlife Service, Jacksonville, FL.

Breininger, D.R., V.L. Larson, D.M. Oddy, R.B. Smith, M.J. Barkaszi. 1996. Demography of Florida scrub-jays in different landscapes. Auk: 113: 617-625.

Breininger, D.R., V.L. Larson, R.W. Duncan, R.B. Smith, D.M. Oddy, M.F. Goodchild. 1995. Landscape patterns of Florida Scrub Jay habitat use and demographic success. Conservation Biology 9: 1442 - 1453.

Breininger, D.M., M.J. Provancha, and R.B. Smith. 1991. Mapping Florida Scrub Jay habitat for purposes of land-use management. Photogr. Eng. and Remote Sensing 57: 1467-1474.

Breininger, D.M., M.A. Burgman, and B.M. Stith. In press. Influence of habitat quality, catastrophes, and population size on extinction risk of the Florida Scrub-Jay. Wildlife Society Bulletin

Brook, B.W., L. Lim, R. Harden, and R. Frankham. 1997. Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island woodhen *Tricholimnas sylvestris* (Sclater). Biological Conservation 82: 119-128.

Brown, J.H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445-449.

Buechner, M. 1987. A geometric model of vertebrate dispersal: tests and implication. Ecology 68: 310-318.

Burgman, M., S. Ferson, and H.R. Akcakaya. 1993. Risk Assessment in Conservation Biology. New York: Chapman & Hall. 314 pp.

Carmen, W. 1989. Behavioral ecology of the California Scrub Jay: a noncooperative breeder with close cooperative relatives. Ph.D. dissertation. University of California, Berkeley, CA. 134 pp.

Caughley, G. 1994. Directions in conservation biology. J. Animal Ecology 63: 215-244.

Conroy, M.J., Y. Cohen, F.C. James, Y.G. Matsino, and B.A. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. Ecological Applications 5: 17-19.

Cox, J.A. 1987. Status and distribution of the Florida Scrub Jay. Florida Ornithol. Soc. Spec. Pub. No. 3.

Christman, S.P. and W.S. Judd. 1990. Notes on plants endemic to Florida scrub. Florida Scientist 53: 52-73.

Dawkins, R. 1976. The Selfish Gene. Oxford: Oxford University Press. 224 pp.

DeGange, A.R., J.W. Fitzpatrick, J.N. Layne, and G.E. Woolfenden. 1989. Acorn harvesting by Florida Scrub Jays. Ecology 70: 348-356.

Doak, D.F., and L.S. Mills. 1994. A useful role for theory in conservation. Ecology 75: 615-626.

Duncan, B., D. Breininger, P. Schmalzer, and V. Larson. 1995. Validating a Florida Scrub Jay habitat suitability model, using demography data on Kennedy Space Center. Photogr. Eng. & Remote Sensing 61: 1361 - 1370.

Dunning, J.B., and D.J. Stewart. 1995. Spatially explicit population models: current forms and future uses. Ecological Applications5: 3-11.

Ebenhard, T. 1991. Colonization in metapopulations: a review of theory and observations. Pp. 105-121 in M.E. Gilpin and I. Hanski (eds.), Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press, London, UK

E.S.R.I. 1990. Understanding GIS. Redlands, CA: Environmental Systems Research Institute, Inc.

Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. J. Wildlife Management 61: 603-610.

Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. Theor. Pop. Biol. 41: 300-314.

Ferson, S. 1991. RAMAS/stage: Generalized Stage-based Modeling for Population Dynamics. Setauket, New York: Applied Biomathematics. 108 pp.

Fishwick, P.A. 1995. Simulation model design and execution: building digital worlds. New Jersey: Prentice-Hall. 448 pp.

Fitzpatrick, J.W., R. Bowman, D.R. Breininger, M.A. O'Connell, B. Stith, J. Thaxton, B. Toland, and G.E. Woolfenden. In prep. Habitat Conservation Plans for the Florida Scrub Jay: A Biological Framework.

Fitzpatrick, J.W., B. Pranty, and B. Stith. 1994. Florida Scrub Jay statewide map. U.S. Fish and Wildlife Service Report, Cooperative Agreement no. 14-16-0004-91-950.

Fitzpatrick, J.W., and G.E. Woolfenden. 1986. Demographic routes to cooperative breeding in some New World jays. Pp.137-160 in M.H. Nitecki and J.A. Kitchell, (eds.), Evolution of Behavior. New York: Oxford University Press.

Fitzpatrick, J.W., G.E. Woolfenden, and M.T. Kopeny. 1991. Ecology and development-related habitat guidelines of the Florida Scrub Jay (Aphelocoma coerulescens coerulescens). Florida Nongame Wildlife Program Technical Report, No. 8. 49 pp.

Florida Atlas and Gazeteer. 1997. (4th ed.). DeLorme, Freeport, Maine.

Forman, R.T.T. and M. Godron. 1986. Landscape Ecology. New York: Wiley.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior 28: 1140-1162.

Hanski, I. 1994. A practical model of metapopulation dynamics. J. Animal Ecology 63: 151-162.

Hanski, I. and M.E. Gilpin 1991. Metapopulation dynamics: brief history and conceptual domain. Pp. 89-103 in M.E. Gilpin and I. Hanski (eds.). Metapopulation Dynamics: Empirical and Theoretical Investigations. London: Academic Press.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Pp. 89-103 in M.E. Gilpin and I. Hanski (eds.), Metapopulation Dynamics: Empirical and Theoretical Investigations. London: Academic Press.

Harrison, S. 1994. Metapopulations and conservation. Pp. 111-128 in P.J. Edwards, R.M. May and N.R. Webb (eds.), Large-scale Ecology and Conservation biology. Blackwell Scientific Publication, Oxford, UK

Harrison, S., A. Stahl, and D. Doak 1993. Spatial models and Spotted Owls: exploring some biological issues behind recent events. Conservation Biology 7: 950-953.

Hooper, R., J.C. Watson, and R.E.F. Escano. 1990. Hurricane Hugo's initial effects on red-cockaded woodpeckers in the Francis Marion National Forest. Trans. 55th N.A. Wildlife and Natural Resources Conference: 220-224.

Howe, R.W. and G. Davis. 1991. The demographic significance of 'sink' populations. Biological Conservation 57: 239-255.

Huston, M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological theory. BioScience 38: 682-691.

Ims, R.A. and N.G. Yoccoz. Studying transfer processes in metapopulations: emigration, migration, and colonization. Pages 247 – 265 in I. Hanski and M.E. Gilpin (eds.), Metapopulation Biology. New York: Academic Press.

Johnson, M.L. and M.S. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Ann. Rev. Ecol. Syst. 21: 449-480.

Judson, O.P., 1994. The rise of the individual-based model in ecology. Trends in Ecology and Evolution 9: 9-14.

Kale, H.W. II, B. Pranty, B. Stith, and C.W. Biggs. 1992. The Atlas of the Breeding Birds of Florida. Final report to Fla. Game & Fresh Water Fish Comm., Tallahassee, FL.

Karieva, P., D. Skelly, and M. Ruckelshaus. 1997. Reevaluating the use of models to predict the consequences of habitat loss and fragmentation. Pages 156-166 in S.T.A. Pickett, R. Ostfels, M. Shachak, and G. Likens (eds.). The Ecological Basis of Conservation. New York: Chapman and Hall.

Kautz, R.S., D.T. Gilbert, and G.M. Mauldin. 1993. Vegetative cover in Florida based on 1985-1989 Landsat Thematic Mapper imagery. Florida Scientist 56: 135-154.

Koenig, W.D., F.A. Pitelka, W.J. Carmen, R.L. Mumme, and M.T. Stanback. 1992. The evolution of delayed dispersal in cooperative breeders. Quarterly Review of Biology 67: 111-150.

Koenig, W.D., D.Van Vuren, and P. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology and Evolution 11: 514 - 517.

Komdeur, J. 1992. Importance of habitat saturation and territory quality for the evolution of cooperative breeding in the Seychelles Warbler. Nature. 358: 493-495.

Krebs, J.R. and N.B. Davies. 1993. An Introduction to Behavioural Ecology (3rd ed.). Blackwell Science, Inc. Cambridge, MA.

Lamberson, R.H., R. McKelvey, B.R. Noon, and C. Voss. 1992. A dynamic analysis of Northern Spotted Owl viability in a fragmented forest landscape. Conservation Biology 6: 505-512.

Lacy, R.C. 1993. VORTEX: a computer simulation model for Population Viability Analysis. Wildlife Research 20: 45-65.

Lande, R. 1988a. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). Oecologia 75: 601-607.

Lande, R. 1988b. Genetics and demography in biological conservation. Science 241: 1455-1459.

Lesica, P., and F. Allendorf. 1995. When are peripheral populations valuable for conservation? Conservation Biology 9: 753-760.

Letcher, B.H., J.A. Priddy, J.R. Walters, and L.B. Crowderl 1998. An individual-based, spatially-explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. Biological Conservation 86: 1-14.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Entomol. Soc. Amer. 15: 237-240.

Levins, R. 1970. Extinction. Lectures on Mathematics in the Life Sciences 2: 75-107.

Lima, S. and P. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11: 131-135.

MacArthur, R. H. and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton, NJ: Princeton University Press. 203 pp.

Mace, G. M., and R. Lande. 1991. Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. Conservation Biology 2: 148-157.

Maley, C. and H. Caswell. 1993. Implementing I-state configuration models for population dynamics: an object-oriented programming approach. Ecological Modelling 68: 75-89.

McCarthy, M.A. 1996. Extinction dynamics of the helmeted honeyeater: effects of demography, stochasticity, inbreeding and spatial structure. Ecological Modelling 85: 151-163.

McCarthy, M.A., D.C. Franklin, and M.A. Burgman. 1994. The importance of demographic uncertainty: an example from the helmeted honeyeater. Biological Conservation 67: 135-142.

McDonald, D.B. and H. Caswell. 1993. Matrix methods for avian demography. Current Ornithology 10: 139-184.

McGarigal, K. and B. Marks. 1994. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Corvallis, OR: Forest Science Dept., Oregon State University.

McGowan, K.J. and G.E. Woolfenden. 1989. A sentinel system in the Florida Scrub Jay. Animal Behavior 37: 1000-1006.

McKelvey, K., B. Noon, and R. Lamberson. 1993. Conservation planning for species occupying fragmented landscapes: the case of the northern spotted owl. Pages 424-452 in Kingsolver, J., P. Karieva, and R. Huey (eds.), Biotic interactions and global change. Sunderland, MA: Sinauer.

Meyers, R.L. and J.J. Ewel (eds.). 1990. Ecosystems of Florida. University of Central Florida Press, Orlando, Florida.

Miller, G.L. and B.W. Carroll. 1989. Modeling vertebrate dispersal distances: alternatives to the geometric distribution. Ecology 70: 977-986.

Mills, L. S., S. Hayes, C. Baldwin, M. Wisdom, J. Citta, D. Mattson, and K. Murphy. 1996. Factors leading to different viability predictions for a grizzly bear data set. Conservation Biology 10: 863-873.

Mooij, W., and D. DeAngelis. 1999. Error propagation in spatially explicit dispersal models. Conservation Biology 11: 1298-1306.

Morrison, M.L., B.G. Marcot, and R.W. Mannan. 1992. Wildlife-habitat Relationships: Concepts and applications. Madison, WI: University of Wisconsin Press.

Mumme, R. and T. Below. In press. Evaluation of translocation for the threatened Florida Scrub-Jay. Wildlife Management.

Mumme, R.J., S.J. Schoech, G.E. Woolfenden, and J.W. Fitzpatrick. In revision. Life and death in the fast lane: demographic consequences of road mortality in the Florida Scrub-Jay. Conservation Biology.

Murphy, D.D. and B.R. Noon. 1992. Integrating scientific methods with habitat conservation planning: reserve design for Northern Spotted Owls. Ecological Applications 2: 3-17.

Noon, B.R. and D.S. McKelvey. 1992. Stability properties of the Spotted Owl metapopulation in southern California. Pages 187-206 in J. Verner et al. (eds.), The California Spotted Owl: A Technical Assessment of Its Current Status. General Technical Report PSW-GTR-133. Albany, California: USDA Forest Service.

Noss, R., m.A. O'Connell, and D.D. Murphy. 1998. The science of Conservation Planning: Habitat Conservation Under the Endangered Species Act. Washington, DC: Island Press. 246 pp.

O'Connell, M. 1994. Preserving scrub habitat. Florida Naturalist 67: 9-12.

Papi, F. (ed.). 1992. Animal Homing. London: Chapman and Hall. 390 pp.

Porter, J.H. and J.L. Dooley. 1993. Animal dispersal patterns: a reassessment of simple mathematical models. Ecology 74: 2436-2443.

Price, M. and M. Gilpin. 1996. Modelers, mammalogists, and metapopulations: designing Stephen's Kangaroo Rat reserves. Pages 217-240 in D. McCullough (ed.), Metapopulations and Wildlife Conservation. Washington, DC: Island Press. 429 pp.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist 132: 652-61.

Pulliam, H.R. 1992. Population dynamics in complex landscapes: a case study. Ecological Applications 2: 165-177.

Pusey, A. and C. Packer. 1987. Dispersal and philopatry. Pages 250 – 266 in B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker (eds.), Primate Societies. Chicago, IL: U. Chicago Press. 578 pp.

Rolstad, J. 1991. Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. Pages 149-163 in M.E. Gilpin and I. Hanski (eds.), Metapopulation Dynamics: Empirical and Theoretical Investigations. London: Academic Press.

Root, K. 1996. Population Viability Analysis for the Florida Scrub-Jay (Aphelocoma coerulescens coerulescens) in Brevard County, Florida. Ph. D. dissertation, Florida Institute of Technology, Melbourne. 199 pp.

Root, K. 1998. Evaluating the effects of habitat quality, connectivity, and catastrophes on a threatened species. Ecological Applications 8: 854-865.

Ruckelhaus, M., C. Hartway, and P. Karieva. 1997. Assessing the data requirements of spatially explicit dispersal models. Conservation Biology 11: 1298-1306.

Rykiel, E. 1996. Testing ecological models: the meaning of validation. Ecological Modeling 90: 229-244.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. BioScience 31: 131-134.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. Ann. Rev. Ecol. Syst. 19: 473-511.

Sjogren, P. 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (Rana lessonae). Pp. 135-147 in M.E. Gilpin and I. Hanski (eds.), Metapopulation Dynamics: Empirical and Theoretical Investigations. London: Academic Press.

Smith, A. 1980. Temporal changes in insular populations of the Pika (Ochotona princeps). Ecology 61: 8-13.

Smith, A. and M. Peacock. 1990. Conspecific attraction and the determination of metapopulation colonization rates. Conservation Biology 4: 320-323.

Soule, M. (ed.). 1987. Viable populations for conservation. Cambridge, UK: Cambridge U. Press.

South, A. 1999. Dispersal in spatially explicit population models. Conservation Biology 4: 1039 – 1046.

Stenseth, N. and W. Lidicker (eds.). 1992. Animal Dispersal: Small Mammals as a Model. New York: Chapman and Hall. 366 pp.

Stith, B.M., J.W. Fitzpatrick, G.E. Woolfenden, and B. Pranty. 1996. Classifying and conserving metapopulations: a case study of the Florida Scrub Jay. Pages 187-216 in D. McCullough (ed.), Metapopulations and Wildlife Conservation. Washington, DC: Island Press. 429 pp.

Swain, H.M., P.A. Schmalzer, D.R. Breininger, K.V. Root, S.A. Bergen, S.R. Boyle, and S.MacCaffree. 1995. Scrub Conservation and Development Plan: Brevard County. Appendix B: Biological Consultant's Report to the Natural Resources Management Division of Brevard County, Florida. August 1995.

Taylor, B. 1995. The reliability of using population viability analysis for risk classification of species. Conservation Biology 9: 551-558.

Thaxton, J.E. and T.M. Hingtgen. 1996. Effects of suburbanization and habitat fragmentation on Florida Scrub-Jay dispersal. Florida Field Naturalist 24: 25-60.

Thomas, C.D. 1990. What do real population dynamics tell us about minimum viable population sizes? Conservation Biology 4: 324-327.

Thomas, C.D. 1994. Difficulties in deducing dynamics from static distributions. Trends in Ecology and Evolution 9: 300.

Thomas, J.W., E.D. Forsman, J.B. Lint, E.C. Meslow, B.R. Noon, and J. Verner. 1990. A Conservation Strategy for the Northern Spotted Owl. Report of the Interagency Scientific Committee to Address the Conservation of the Northern Spotted Owl. Portland, Oregon: U.S. Fish and Wildlife Service. 427 pp.

Turner, M.G., G.J. Arthaud, R.T. Engstrom, S.J. Hejl, J. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit population models in land management.. Ecological Applications 5: 12-16.

Turchin, P. 1998. Quantitative Analysis of Movement. Sunderland, MA: Sinaeur.

U.S. Fish and Wildlife Service. 1991. Floridians advised of Scrub Jay conservation measures. June 18. News Release. Jacksonville, FL.

Waser, P.W. 1985. Does competition drive dispersal? Ecology 66: 1170-1175.

Waser, P.W., S.R. Creel, and J.R. Lucas. 1994. Death and disappearance: Estimating mortality risks associated with philopatry and dispersal. Behavioral Ecology 5: 135-141.

With, K., R. Gardner, and M. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos 78: 151-169.

Wolff, W.F. 1994. An individual-oriented model of a wading bird nest colony. Ecological Modelling 72: 75-114.

Woolfenden, G.E. and J.W. Fitzpatrick. 1984. The Florida Scrub Jay: Demography of a Cooperative-breeding Bird. Monogr. Pop. Biol. no. 20. Princeton, NJ: Princeton University Press.

Woolfenden, G.E. and J.W. Fitzpatrick. 1986. Sexual asymmetries in the life history of the Florida Scrub Jay. Pp. 87-107. In D. Rubenstein and R.W. Wrangham (eds.), Ecological Aspects of Social Evolution: Birds and Mammals. Princeton, NJ: Princeton University Press.

Woolfenden, G.E., and J.W. Fitzpatrick. 1991. Florida Scrub Jay ecology and conservation. Pp. 542-565 in C.M. Perrins, J.D. Lebreton, and G.J.M. Hirons (eds.), Bird Population Studies: Relevance to Conservation and Management. Oxford, UK: Oxford University Press.

Woolfenden, G.E. and J.W. Fitzpatrick. 1996. Florida Scrub-Jay (*Aphelocoma coerulescens*). In A. Poole and F. Gill (eds.), The Birds of North America, No. 228. Philadelphia: The Academy of Natural Sciences, and Washington, DC: the American Ornithologists' Union.

Wooton, T.J. and D.A. Bell. 1992. A metapopulation model of the Peregrine Falcon in California: viability and management strategies. Ecological Applications 2: 307-321.

Zack, S. 1990. Coupling delayed breeding with short-distance dispersal in cooperatively breeding birds. Ethology 86: 265-286.

Zar, J.H. 1996. Biostatistical Analysis (3rd ed.). New Jersey: Prentice Hall. 662 pp.

Zollner, P.A. and S.L. Lima. 1999. Search strategies for landscape-level interpatch movements. Ecology 80: 1019 – 1030.

BIOGRAPHICAL SKETCH

Bradley M. Stith was born in Indianapolis, Indiana, but moved to Sarasota, Florida, at the age of three. He spent most of his youth there, collecting reptiles, scuba diving, and exploring the many wild areas around Sarasota. With his growing love of nature came the sad realization that humans were rapidly destroying the playground of his youth. His interest in conservation issues were put on hold for awhile as he obtained a B.S. in geology in 1980 from the University of Arizona in Tucson. He then moved to Houston, Texas and worked for a small consulting firm that developed and marketed computer mapping software (now known as GIS), and built digital databases used primarily by the oil industry. His job as programmer/software installer/trainer allowed him to travel around the U.S. and overseas. By 1986 the economy in Texas became badly depressed, and he decided to seek a graduate degree. He entered the graduate program in the Department of Wildlife and Range Sciences at the University of Florida in 1987. He immediately began work on the Florida Breeding Bird Atlas under Dr. Stephen R. Humphrey. In 1990 he completed his thesis entitled "Satellites, Landscapes, and GIS: A Case Study in the Atlantic Forest of Brazil" and obtained a Master of Science degree. He then re-enrolled as a Ph.D. student in the same program, now known as the Department of Wildlife Ecology and Conservation and will receive his Ph.D. in 1999.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy

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Professor of Wildlife Ecology and Conservation

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